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C O N T E N T S

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INTRODUCTION

In 1917 Tillyard brought together all the scattered information regarding the morphology as well as other biological studies of dragonflies in a book entitled "The Biology of Dragonflies." His discussion of morphology in this book was based on the writings of previous workers who were mainly interested in comparative studies of certain organs. Since this date some morphological characters have been further and well investigated but other structures remain inadequately studied. Furthermore, entomologists working on dragonflies have paid little attention to the new interpretations given by Ferris (1939, 1940), Snodgrass (1947), and others on the fundamental structures of certain parts of the body of insects in general. There is not a single species of dragonfly that has been studied critically in the light of the most recent morphological interpretations.

The purpose of the present study is fourfold: (1) to bring into unity all the different terminologies which have been used in morphological and taxonomic work on dragonflies; (2) to apply the knowledge of the most recent morphological interpretations; (3) to bring out some new interpretations of morphological characters which the author believes to be inadequately or errone-

ously treated previously; and (4) to serve as a contribution to the morphology of dragonflies, especially as a foundation for future taxonomic studies.

Onychogomphus ardens Needham (Gomphidae) has been selected for study for three reasons. (1) It belongs to the primitive family Gomphidae of the order Odonata. This family is well represented by genera and species in my own collection which will be used for future taxonomic studies. (2) Specimens of this species are of large size and therefore relatively easy to study. (3) It is rather common in South China.

HEAD (Pl. 1)

The head of Onychogomphus ardens Needham is hypognathus and somewhat anteroposteriorly flattened, the anterior aspect being convex and the posterior aspect being concave. Posteriorly it is attached to a narrow neck. The female differs from the male in having a pair of occipital horns (Fig. 2: OCCH) on the occipital margin.

The areas generally referred to as frons, vertex, and occiput by earlier workers are designated as such in this paper. No attempt has been made to change their names although they have been interpreted differently by modern morphologists (DuPorte, 1946; Snodgrass, 1947). The old designations are used here without modification to avoid further confusion in taxonomic work.

Sutures of the cranium or capsule

The principal sutures of the cranium are postocellar, epistomal, subgenal, ocular, parafrontal, postoccipital, and clypeal sutures.

The postocellar suture (POS) is a transverse suture which separates the vertex from the occiput. It lies between the two compound eyes at their closest points. According to Lew (1933) this suture is secondarily developed

and is not homologous with the epicranial suture (e.g. Garman, 1917) of other insects. This suture is designated by Lew as postocular suture; but unfortunately in the same paper he created another term, the postocellar suture, evidently referring to the same structure. The latter term is probably the one he meant to use, while the former term might be a typographical error, since it is definitely not decriptive of its position. Snodgrass (1947), however, mentioned: "The cleavage line on the head of larval Odonata is characteristically T-shaped rather than Y-shaped, inasmuch as the frontal arms usually go almost straight laterally." In the present species the postocellar suture represents the transverse bar of the T and therefore corresponds to the frontal arms.

The epistomal suture (ESS), or fronto-clypeal suture, is a distinct and almost straight line across the anterior part of the cranium. Along this suture a strong epistomal ridge (ESR) is produced internally.

The subgenal sutures each consists of two portions, the pleurostomal and hypostomal sutures. The pleurostomal suture (PMS) marks the lateroventral margin of the capsule above the mandibular bases and between the anterior (AAR) and posterior articulations (CAR) of each. Along this suture the anterior tentorial arm (ATA) is produced in-

ternally, and to it a narrow sclerite, the pleurostoma (PM) is attached. The poorly defined hypostomal sutures (HMS) each follows closely the posterior margin of the cranium between the posterior articulation of the mandible (CAR) and the posterior tentorial pit (PTP).

The ocular sutures (OS) surround the bases of each of the compound eyes except in the anterior aspect of the head where a narrow band of sclerite, the ocular sclerite (OCS), is interposed between them.

Parafrontal sutures (PFS) are present, one on each side of the frons. Apparently no name has previously been given to them although they are shown in many drawings of various species of dragonflies by different authors (e.g., Tillyard, 1926; Lew, 1933). These are probably the frontogenal sulcus of DuPorte (1946) or lateral grooves of Snodgrass (1947). Each suture extends from the middle of the inner margin of the eye near the antenna to the anterior articulation of the mandible, thus separating frons from gena. Each is hidden by the lateral portion of the elevated frons and clypeus and therefore is invisible in the anterior aspect of the head. Along this suture a low ridge is produced internally.

The postoccipital suture (POCS) closely parallels

the dorsal and lateral margins of the foramen magnum (FM).

The clypeal suture is absent, but its position is indicated by a distinct line of demarcation between the sclerotized postclypeus and the mostly membranous anteclypeus.

The antennal socket is well defined but is not circumscribed by an antennal suture.

Areas of the cranium

The principal areas of the cranium are clypeus, frons, vertex, occiput, genae, postocciput, postgenae, pleurostomae, hypostomae, and eyes. The gula is absent in this species. However, it has been very vaguely indicated as being present in the order Odonata by earlier workers. Calvert (1893) said that the gula was membranous: Tillyard (1917) probably concurred with him in this matter. Marshall (1914) probably wrongly designated submentum as gula.

The clypeus is a large transverse sclerite differentiated into a light-colored, mostly membranous anteclypeus and a black-colored, sclerotized postclypeus. The latter areas are separated by deep indentations on both sides. The anteclypeus (ACL) is light colored, laterally produced into a lobe-like structure, with a narrow sclerotized

piece on each side extending mesally from the tip of the lobe a distance of one-third the width of the anteclypeus. The postclypeus (PCL) is black, with or without a small transverse light-colored spot on each side. It expands laterally and extends ventrally thus overlapping a portion of the lateral lobe of the anteclypeus. A small condyle, the anterior articulation of mandible (AAR), is produced on each side near the base of the postclypeus. It is covered by the laterally expanded portion of the postclypeus so that it cannot be seen in the anterior aspect of the head.

The frons (FR) is a large, transverse, convex area which is bounded ventrally by the epistomal suture, laterally by the parafrontal sutures, and dorsally by a transverse furrow between it and the vertex. It is differentiated by a sharp fold into an upper horizontal portion and an anterior or vertical portion, but there is no sutural demarcation between these regions. The upper portion is called the top of frons (TFR) which is differentiated into two low prominences separated by a broad median furrow. A broad transverse light-colored stripe covers most of the top as well as a part of the anterior portion of the frons. This stripe is sometimes separated in the middle along the median furrow. In this light-colored area there are a

few small black tubercles each of which bears a minute hair.

The vertex (V) is a trapezoidal area bounded ventrally by a groove between it and the frons, dorsally by the post-ocellar suture, and laterally by the ocular sutures. It bears a pair of antennae and three ocelli (OC), the latter being very large. The deeply sunken middle ocellus is a little lower in position than the lateral ocelli. Along the dorsal rim of the middle ocellus there is a very low but large knob-like tubercle which bears a group of fine and wavy long hairs. External to the tubercle and the lateral ocellus there is a subsemicircular ridge. The dorsal tentorial pits (DTP) are present as a pair of semi-circular sutures above and lateral to the bases of the antennae (mostly obscured by the antennae in anterior view and by the eye in lateral view). It is interesting to point out here that the dorsal tentorial pits are present in the adult dragonflies (Lew, 1933) whereas they are usually represented by a pair of callosities in the dragonfly nymphs and many insects. Two peculiar papillae (PA), about two-thirds as long as the third antennal segment, situated one on each side very close to the external rim of the antennal socket, are present in both sexes. They are small and usually obscured from view by the antennae

and therefore are easily overlooked. Apparently they have not been reported heretofore. They occur also in Onychogomphus micans Needham which is very closely related to the present species, but not in Ictinogomphus rapax (Rambur) (Gomphidae) and Anax nigrofasciatus Oguma (Aeschnidae) which I have examined.

The furrow which separates the frons from the vertex is called frontal furrow or frontal suture by Tillyard (1917). These terms are confusing since the structures they define are definitely not homologous with the frontal sutures of other insects. Morphologically speaking (DuPorte, 1946; Snodgrass, 1947), the areas of the frons, vertex, and occiput described here are not homologous with those of other insects or even with these areas as designated in certain other species of dragonflies, althouth they are generally so considered by students of Odonata.

The occiput (OCC) is situated on the top of the head between the compound eyes. In the anterior aspect of the head it appears as a transverse area bounded ventrally by the postocellar suture, laterally by the compound eyes, and dorsally by the occipital border, or occipital margin (OCCM), which is almost twice as wide as the postocellar suture, and fringed with long black hairs. In the female

there is a pair of occipital horns (OCCH) on the occipital margin. These are not to be confused with a pair of similar horns which arise on the vertex above the lateral ocelli and which are also, but erroneously, called the occipital horns. Such horns occur in a number of species of the family Gomphidae, e.g., Gomphus flavicornis Needham (Lew, 1933, pl. viii, fig. 9), Gomphus cuneatus Needham, and Davidius bicornutus Selys. The posterior aspect of the occipital region is called the rear of the occiput (ROOC). It is a subquadrate area situated above the foramen magnum, with a large light yellow colored marking in the center. Laterally it is demarked with weakly defined furrows or wrinkles which indicate the dividing line between it and the postgenae.

The genae (G) are small sclerites. Dorsally each gena is bounded by the parafrontal and the ocular sutures, and ventrally to its evaginated margin is attached a small transverse sclerite, the pleurostoma (PM).

The postgenae (PG) are a pair of large sclerites one on each side of the posterior aspect of the head. The outer margin of each postgena which borders the eye is notched at about the center. Mesally and mesoventrally the postgena is bounded by the postoccipital suture and

hypostomal suture respectively. Ventrally it is fused with the gena. This fused portion bears the posterior articulation of the mandible.

The postocciput (POOC) is a roughly horseshoe-shaped narrow sclerite surrounding the dorsal and lateral sides of the foramen magnum, with its ends terminating at the posterior tentorial pits (PTP) where a pair of small transverse processes, the occipital condyles (OCCD) are produced toward each other. On each side of the foramen magnum the postocciput is produced mesally into a short process.

The pleurostomae (PM) are very small transverse sclerites, one on each side, situated in the evaginated ventral margin of the gena between the anterior and the posterior mandibular articulations.

The hypostomae (HM) are narrow bands or thickenings one on each side bordering the lower margin of the postgena between the posterior articulation of the mandible and the posterior tentorial pit.

The compound eyes (EYES) are large, their closest distance being along the postocellar suture. Each is evaginated in the middle on its posterior margin as shown in Figs. 4 and 5.

Tentorium (Figs. 4-6)

The tentorium consists of a corpotentorium and three pairs of tentorial arms; namely, dorsal, anterior, and posterior arms.

The corporotentorium (CT), or tentorial body, is a transverse bar very close to the posterior surface of the head capsule and appearing as the floor of the foramen magnum. Apparently it is often mistaken for the gula by some students of Odonata.

The posterior tentorial arms (PTA) arising from distinct posterior tentorial pits (PTP) are very short and are not differentiated from the corporotentorium.

The anterior tentorial arms (ATA) arise from extremely elongated tentorial pits lying along the entire lengths of the pleurostomal sutures. Each anterior tentorial arm is a fan-like structure strengthened by three heavily sclerotized ribs radiating from the corporotentorium. The posterior rib (PRB) extends to the posterior mandibular articulation, the middle rib (MRB) to the anterior mandibular articulation, and the anterior rib (ARB) to the lateral end of the epistomal ridge. On the ventral surface of the middle rib there are two processes: The anterior

process is called the mandibular process (MDP) and consists of a very large ovoid tendon-like structure with a short narrow stalk. The large ovoid portion is inserted in the heavy muscles of the mandible. The posterior process is called the maxillary process (MXP) and is a long and slender tendon supplying attachment for the maxillary abductor muscles. On the posterior rib there is also a short process.

The dorsal tentorial arms (DTA) each consists of a simple flattened structure arising from the middle rib of the anterior tentorial arm. Each narrows slightly in the middle and apically fused firmly with the invagination of the dorsal tentorial pit.

Head appendages (Pls. I-III)

The movable parts of the head are the antennae, labrum, mandibles, maxillae, hypopharynx, and labium.

The antennae (ANT) are short, inconspicuous, setaceous, and 4-segmented. The basal segment, or scape (S), is very thick. The second segment, or pedicel (P), is subequal in length and about half the diameter of the preceding segment. The third and the last segments are collectively called flagellum (FL), or distalia, which

is slender and bristle-like; the third segment being about two-thirds as long as the pedicel; the last segment being longer than the other three segments combined.

The labrum (LR), or upper lip, is a transverse sub-ovoid sclerite, movably attached to the anteclypeus and functions as one of the mouthparts. It is generally regarded as not a true appendage. Great differences of opinion exist among entomologists as to its homology. For more detailed accounts the reader is referred to recent papers by Ferris (1947) and Henry (1948). Aborally (Fig.7) it is slightly convex, black, with two large ovoid yellow spots, and fringed with many long hairs along its distal and lateral margins. Adorally (Fig. 8) it has a flat surface, is black on lateral regions, and has a large clear area called the epipharynx in middle. The epipharynx (EPX) consists of a round, slightly depressed, sclerotized area in the center surrounded by a group of small circular tubercles and hairs. These tubercles are probably taste organs. Some hairs are grouped together to form the brushes (BH) pointing mesad.

The mandibles (MD) are very strong unsegmented appendages bearing strong teeth which may be divided into two groups: a large basal mola (MO) and a distal group of three

incisors (ICS).

The base of the mandible is triangular in shape, with one lateral and two mesal angles. The mesal angles are designated as inner and outer. The mandible is attached to the head capsule by two articulations, the ginglymoid anterior articulation (AAR) at the outer angle and the condylic posterior articulation (CAR) at the lateral angle. A strong flexor tendon (FT) is attached to the inner angle and a weak retractor tendon (RT) to the lateral angle.

The adoral side (Fig. 10) of the mandible has two tuberculate and hairy areas, one at the base of the incisors and the other parallel to the margin of the mola; the former area being crescent-shaped. The aboral (Fig. 9) side of the mandible has a similar crescent-shaped, tuberculate, and hairy area which is silghtly depressed and joins with a ridge extending to the anterior articulation.

The three incisors (ICS) are of unequal length; one of them being very long, sharply pointed, slightly curved, and bearing the smaller basal one on its mesal edge and an even still smaller medial one on its adoral side. The mola (MO) has four cusps set on a broad base in the shape of a Z on the right mandible and an inverted Z (⅄) on the

left mandible. The cusps are placed one at each end and one at each angle of the Z.

The maxillae are composed of several parts: namely, cardo, stipes, inner lobe, and outer lobe.

The cardo is an elongate structure internally strengthened by an X-shaped ridge, the mesal arms of the X being submarginal and the lateral arms marginal. It is divided into basicardo (BCD) and disticardo (DCD) by a suture which is situated along the lateral margin of the basolateral arm and the mesal margin of the distomesal arm. The concave area of the basicardo between the basal arms is about two-thirds as large as the weakly sclerotized convex area of the disticardo between the distal arms; the latter area being adorned with a few long hairs.

The stipes (STI) is a large elongate rectangular structure adorned laterally with many short hairs on its inflected area and apically with many long hairs. A mesal submarginal sutural groove (SG) (Snodgrass, 1935) sets off a narrow area called parastipes (Crampton) (SG). An isolated sclerite is present in the membrane which attaches along the margin of the lateral inflected area. Nothing is known about this sclerite although it has been shown in drawings by earlier workers (e.g., Tillyard, 1917,

p. 16, fig. 4).

The inner lobe (IL) and the outer lobe (OL) are two freely movable processes, the former being generally regarded as representing the fused lacinia and galea of more typical mandibulate insects, and the latter, the palp.

The inner lobe (IL) is a large process basally fused with the stipes but separated from the parastipes by a narrow strip of membrane. Basally it is expanded on its mesal portion and adorned with many long hairs. Apically it is narrowed and gently curved, ending in three teeth pointing mesad, the apical tooth being very long and the middle one the smallest. The weakly sclerotized area along the mesal margin of the apical half of the inner lobe bears three widely spaced teeth of subequal length, also pointing mesad.

The outer lobe (OL) is a stout, slightly curved, fingerlike structure, about as long as the inner lobe, with the lateral portion of the basal half weakly sclerotized and unpigmented. Basally it is situated on a small transverse sclerite on the adoral side of the maxilla.

The hypopharynx is a large, elongate, wedge-shaped lobe in the preoral cavity, apparently consisting only of the lingua, with its aboral surface (Fig. 11) about half as

long as its adoral surface (Fig. 12), its lateral sides slightly divergent, and its apical margin slightly emarginate.

Adorally (Fig. 12) the hypopharynx is adorned with hairs. Those hairs along the distal margins and surrounding the subapical, depressed sclerotized area are very long and widely spaced. Basally the hypopharynx has a heavily sclerotized transverse bar which is fused laterally with a pair of slightly raised sclerotic structures immediately distal to it; the former with a low transverse internal ridge, and the latter with a number of small round nodules. A single transverse, raised, somewhat wrinkled, weakly sclerotized structure, and a pair of similar smaller ones are situated distal and lateral to the sclerotized structures respectively.

Aborally (Fig. 11) the lateral walls of the hypopharynx contain a pair of basal plates, the apical ends of which are attenuate, whereas the basal ends expand and extend along the basal margin of the hypopharynx to the salivarium (SAL).

The labium consists of the following movable parts: submentum, mentum, middle lobe, squames, lateral lobes, and movable lobes.

The submentum (SM) is a quadrangular piece with its basal margin slightly evaginated and its lateral edges subparallel to each other. Basally it is bounded by membrane continuous with the neck region. Laterally and adorally it is connected with the mesal margins of the cardines and stipites of the maxillae and with the base of the hypopharynx by a large membrane.

The mentum (MN) is a transverse area. Adorally (Fig. 16) it is partly membranous, with a pair of large transverse subrectangular sclerites imbedded in the membrane. These sclerites are adorned with long hairs on their bulging lateral portions. Apically the mentum is separated from the middle lobe by a distinct membranous fold. Aborally (Fig. 15) it is sclerotized on its basal half and weakly so on its distal half; with distinct line of demarcation between these regions. The basal half is fused laterally with the squames. The distal half is unpigmented, adorned with a few scattered microscopic hairs, and fused distally with the middle lobe. Distolaterally it is evaginated into a socket-like structure on each side to which the mesobasal portion of the lateral lobe is attached.

The middle lobe, or median lobe (ML), is a large

subrectangular piece which, according to Butler (1904), corresponds to the ligula of other insects. The latter term is not to be used, because a part of the pronotum is also called the median lobe. Adorally (Fig. 16) it is weakly sclerotized and pigmented on its apical third and narrowly so along its lateral portions, with long hairs on these areas: the remaining area is unpigmented and adorned with a few scattered microscopic hairs.

The squames (SQ) are a pair of convex sclerites, which, according to Tillyard (1917), correspond to the palpigers (The term squames is rather confusing since it has been used to designate different structures in different orders of insects.). Aborally (Fig. 15) they are subrectangular in shape, mesobasally fused with the basal portion of the mentum, laterally deflected to approach the sclerites of the mentum on the adoral side.

The lateral lobes (LL) are a pair of hairy sclerotized structures attached to the squames and mentum, with their mesal margins straight and their lateral margins strongly convex. Each lobe is produced mesoapically into a very long, bare, and sharp end hook (EH) pointing meso-orally. Lateral to the end hook is an even longer hairy movable hook (MH) with tis basal half about twice as wide as its apical half.

CERVIX (Pl. IV)

The cervix (sometimes called neck or microthorax) is a region between the head and the prothorax, narrow anteriorly, mainly membranous, with lateral, dorsal, and ventral cervical sclerites. The lateral cervical sclerites are the largest and serve as pivots for the head while the other sclerites are mostly small and completely surrounded by membrane.

The lateral cervical sclerites each consists of a basal postcervicale (PC) and a distal eucervicale (EC) (Crampton, 1926) forming a hinge at their juncture. The postcervicale is V-shaped, fitting between the pronotum and the episternum, with the arms of the V pointing anteriorly. The eucervicale is incompletely divided into a dorsal and a ventral portion by a deep and narrow incision. The anterior half of the dorsal portion of the eucervicale is unpigmented and whitish. The ventral portion is somewhat twisted, produced mesad and then anteriorly into a long process called the cephaliger (CEP): the latter lies freely inside the cervical membrane, with its apex connected with the occipital condyle (Fig. 3, OCCD).

There are two transverse dorsal cervical sclerites (DC) in the middle of the cervix, with a pair of small

and weakly sclerotized sclerites between them; the posterior transverse sclerite also being weakly sclerotized. Another pair of dorsal sclerites is situated on the posterior margin of the cervix: they are fairly large in size, well sclerotized, and partly obscured dorsally by the anterior lobe of the pronotum.

The paired ventral cervical sclerites (VC) are roughly L shaped, with the transverse bars of the Ls almost touching each other, and the other ends of the Ls being in contact with the occipital condyles. There is a small weakly sclerotized area attached at the angle of the L, with many tiny tubercles each bearing a microscopic hair.

THORAX

The thorax is differentiated into two distinct parts, namely a small prothorax and a large synthorax (the latter also called pterothorax) representing the fused meso- and metathorax.

PROTHORAX (Pl. IV)

The prothorax is a small segment, narrow anteriorly, with its length subequal to the vertical diameter of its anterior end which is about two-thirds that of its posterior

end. The pronotum (Figs. 17, 19) covers the dorsal half of the segment, topographically differentiated into anterior, median, and posterior transverse lobes alternated with two furrows where ridges are produced internally. The anterior lobe (AB) has its anterior margin whitish. The anterior furrow is deep and about as broad as the anterior lobe, laterally with a depression on each side where a long pointed apodeme is produced internally. The median lobe (MB) is divided into two parts by a narrow median sagittal groove. It is minutely tuberculate in the areas on both sides of the median groove and on its lateral portions and with a similar but smaller area between them. The lateral tuberculate areas are adorned with fine, long, and wavy hairs. A large semicircular depression is situated at the anterior end of the median groove and gives rise to an internal apodeme which is long, slightly curved, narrow in the middle, and expanded distally into a discoidal structure. The posterior lobe (PB) is somewhat like a Cupid's bow in shape on its dorsal aspect, dorsally minutely tuberculate, and with long, fine, wavy hairs all over.

The propleura (Fig. 19) each consists of two approximately equal-sized sclerites, the episternum and the epimeron, separated by the pleural suture (PLS_1) which is almost perpendiculat to the long axis of the body. Along

the pleural suture a low ridge, or lateral apodeme is produced internally. The episternum (ES_1) is a transverse piece, narrow in the middle, with its dorsoanterior angle fused with the sternum, and its posterior portion slightly bulging. It is minutely tuberculate all over, with the bulging area having larger tubercles and long wavy hairs. The epimeron (EM_1) is a rectangular piece, slightly higher than wide, tuberculate only on its ventroposterior portions, dorsally produced into a narrow strip along the posterior border of the pronotum to approach closely the lateral end of the posterior lobe.

The prosternum (Fig. 18) consists of an anterior, large, elongate, rectangular piece and a posterior pair of small sclerites, the latter collectively termed the furcasternum (PFST) (Crampton, 1926). The rectangular piece is divided into two portions, the anterior basisternum (BS) and the posterior furcasternum (FS), by an anteriorly arched sternacostal suture (SCS) which ends at the large furcal pits (FP), or apophyseal pits (Ferris, 1940). Along the sternacostal suture a ridge is produced internally.

The basisternum is fused on its anterior angles with the episterna. It is minutely tuberculate, with a broad, shallow, submarginal circumscribing depression; the posterior course of the depression being weakly sclerotized

and unpigmented. The area between the posterior depression and the sternacostal suture is raised, with long hairs along its anterior margin. The central area of the furcasternum (FS) between the furcal pits and the sternacostal suture is protuberant and rather coarsely tuberculate. The furca (F_1) consists of a pair of large inverted foot-shaped apodemes widely separated from each other; each arm with a long narrow tendon at its apex.

SYNTHORAX (Pls. V, VI)

The synthorax, or pterothorax, is composed of the fused meso- and metathorax, ventrally carrying two pairs of legs on its anterior half, and dorsally two pairs of wings on its posterior half. The pleura are very large while the terga and the sterna are very small.

Terga (Figs. 21, 22)

The terga are connected with the pleura only by membranes. They are not connected with the latter by prealares anteriorly or by postnotum posteriorly, such as is the case in most other winged insects. Thus, it would seen that the terga can move up and down without distortion during flight.

The anterior most part of the mesotergum is roughly a T-shaped structure divided into the acrotergite (ATG) and the prescutum (PSC_2) by the antecostal suture (ACS) along which a pair of small phragmata is produced internally. The ends of the transverse bar of the T are the prealares (PRA) which serve, in the present species, as pivots for the anterior lobes of the humeral plates (HP), and, are connected posteriorly with the detached plates of the scutum (Snodgrass, 1935) to be described later.

The scutum (SCT_2) is a large, somewhat ovoid, convex structure, wider posteriorly, with a large, central portion weakly sclerotized and unpigmented. Anteriorly the lateral portion of the scutum is detached into a bilobed plate which is fused with the prealare. Posteriorly the adanal sclerite, or posterior notal wing process (PWP), is narrowly separated from the scutum by a incision and is articulated with the axillary plate. The detached plate of the scutum has been shown by Snodgrass (1929, Fig. 11, A, a; 1935, Fig. 123, B, a), but its importance in the wing mechanics has not been well investigated. It consists of two lobes, the anterior suralare sclerite, or anterior notal wing process (AWP), and the posterior adnotal sclerite, separated by the notal incision, or the lateral emargination. Near the mesal

margin of the detached plate there is a groove along which an apodeme (AP) is produced internally. The latter is a large, elongate structure, apically expanded into an irregularly elongate plate which is constricted in the middle. This apodeme is called cap-tendon by earlier workers (Calvert, 1893; Tillyard, 1917). To this apodeme the principal elevator muscle is attached. Two more small sclerites are present. One of these is the first axillary (IAX), also called notal ossicle, notale, or notopterale. It is elongate triangular, situated along the mesal margin of the humeral plate, and mostly obscured by the latter in dorsal view. The other small sclerite, distinct from the adnotal sclerite in this species, is situated between the latter and the anteromesal margin of the axillary plate. A preliminary study of Anax junius, a common American species (Aeschnidae), shows a condition in which the detached plates are not fused with the prealares and the axillary sclerites are not independent from the anterior notal wing processes. The importance of the detached plates of the scutum and the axillary sclerites morphologically and phylogenetically in the wing mechanism will be discussed later.

The scutellum (SCL_2) is a comparatively small, convex, transverse, ovoid sclerite from the posterolateral angle of which the corrugated axillary cords (AXC) are produced.

A small transverse sclerite is closely applied to and partly fused with the anterior margin of the axillary cord. Along the line of fusion a low ridge is produced internally and to it the postscutellum ($PSCL_2$) is articulated.

The postscutellum ($PSCL_2$) (= acrotergite, Whedon, 1938) is even larger than the scutum. It is a subrectangular sclerite, pigmented laterally only, separated by an internal V-shaped ridge into three regions which are probably inaccurately termed median postscutum and lateral postscutella by Tillyard (1917).

The anteriormost part of the metatergum is a narrow transverse sclerite, the prescutum (PSC_3), with a submarginal suture along which a low ridge is produced internally. It is connected by a tiny linear sclerite on each side.

The scutum (SCT_3) is a large transverse sclerite with rounded anterior angles. Its central portion is weakly sclerotized and unpigmented. A small spine-like apodeme is produced internally from a pit which is situated very close to its anterior margin. Laterally the suralar, adnotal, and adanal sclerites are not separated from the scutum (also true in Anax junius).

The scutellum (SCL_3) and the axillary cords (AXC) are similar to those of the preceding segment, except that the latter structures are divergent posteriorly in the metathorax.

The postscutellum ($PSCL_3$) is mainly weakly sclerotized, unpigmented, and merged with the membrane between it and the first abdominal tergite, except for a trace of sclerotized area on each side posterior to the axillary cord.

Pleura (Fig. 21)

The pleura of the synthorax are very large and greatly modified. Laterally the synthorax has two oblique sutures, the mesothoracic pleural (PLS_2) and the metathoracic pleural (PLS_3) sutures, located between the coxae and wing bases of their respective regions. On the lower portion of the synthorax between the two pleural sutures is a transverse ovoid spiracle, the posterior spiracle, or metastigma (IIISP). Just anterior to the metastigma is a short slanting suture, the middle lateral suture (MLS) which represents the remnant of the intersegmental suture (Snodgrass, 1909).

Different names have been used by various taxonomic workers to designate the above mentioned sutures as follows:

Mesothoracic pleural suture

= Humeral suture (Calvert, 1893; Needham, 1903, 1930; Tillyard, 1917; Fraser, 1933).

= First lateral suture (Needham, 1903, 1930).

Intersegmental suture (Snodgrass, 1909)

= Interpleural suture (Tillyard, 1917).

= Middle lateral suture, or middle suture (Needham, 1930).

= First lateral suture (Rambur; Calvert, 1893; Tillyard, 1917).

= Second lateral suture (Needham, 1930).

= Antero-lateral suture (Fraser, 1933).

Metathoracic pleural suture

= Second lateral suture (Calvert, 1893; Tillyard, 1917).

= Third lateral suture (Needham, 1930).

= Postero-lateral suture (Fraser, 1933).

The course of the mesothoracic pleural suture (PLS_2) is crooked, with its lower one-fourth almost perpendicular to the longitudinal axis of the body, its upper three-fourths slightly bowed and slanting posteriorly, and with a short portion between them smoothly curved. The angle of skewness is 60 degrees and the angle of tilt of wing

bases is 32 degrees in the present species. These angles are greater than the corresponding angles in any gomphine dragonfly measured by Needham and Anthony (1903). Needham and Anthony defined the degree of skewness or inclination (also called angle of humeral suture) as the acute angle between the suture and an imaginary line perpendicular to the longitudinal axis of the body, and the angle of tilt of wing bases as the acute angle between a line drawn through the wing bases and the longitudinal axis of the body. It must be pointed out that Tillyard (1917) used the term angle of obliquity in synonymy with skewness, both of which he defined as angle of tilt of wing bases. This must not be confused with the angle of skewness of Needham and Anthony.

The metathoracic pleural suture (PLS_3) has almost the same shape as the preceding one except that its lower one-fourth is a little slanting plsteriorly instead of almost perpendicular to the longitudinal axis of the body, and its upper three-fourths is almost straight.

Particular attention is here given to the courses of the pleural sutures and the relative positions of the wings and the legs. The older view as to the phylogenetic origin of the orientation of these parts is well expressed by Tillyard (1917, 1926), Imms (1948), and others who maintain

that the great development of the mesothoracic anepisterna "pushes" the wings backward away from the head, carrying the terga with them, and that the correlated growth of the metathoracic epimera "pushes" the sterna and the legs forward so that the latter come into position close behind the mouth. However, judging from the courses of the pleural sutures, it is believed that the vertical positions of the lower portions of the pleural sutures (a condition usually considered to be primitive) probably indicate the primitiveness of this region while the posteriorly slanting position of their upper portions probably indicate the evolutionary enlargement of the upper portion of the synthorax. The static nature of the lower region indicates that the legs have not been "pushed" forward, while the posteriorly slanting position of the upper region indicates that the wings have moved backwards away from the head, to a position at or near the center of gravity of the greatly elongated body of the insect.

Regarding the positions of the three pairs of legs, it is interesting to note that the knee joint between the femur and the tibia of the prothoracic leg is directed sidewards, that of the mesothoracic leg, sidewards and backwards, while that of the metathoracic leg, backwards. The pleurocoxal articulation of the metathoracic leg indicates a rota-

tion of its axis of about 90 degrees. The result of the rotation of the metathoracic legs might be of definite advantage to the insect in catching prey during flight or in perching on the twig. The legs are not fitted for walking but they serve very well for climbing when that mode of progress is required.

The mesothoracic episternum is divided by an inverted V-shaped suture into anepisternum and katepisternum. The anepisternum (AES_2) is greatly expanded and meets with the corresponding part of the other side of the thorax along the mid-dorsal line to form a ridge, the dorsal carina (DCR), anterior to the wing bases. At the anterior end of the dorsal carina there is a transverse ridge, the collar (COL), which is adorned with fine wavy hairs. On the dorsal aspect of the synthorax the area between the collar and the wing bases is called the front of synthorax. At about the middle of the front of synthorax the dorsal carina is raised into a sharp point. Posterior to this point the carina is divided into two low ridges which are parallel for a short distance and then widely divergent. These ridges are collectively called the antealar ridge (ARG), or crest. The area posterior to the ridge is called the antealar sinus (AAS). Anterior to the collar there is a transverse sclerite, the spiracular dorsum (SPD), which

is medially invaginated to form a horn-like apodeme. The deflected portions of the spiracular dorsum are called mesostigmatic laminae (MSL). Each lamina bears an anterior spiracle, or mesostigma (IISP). A preliminary study of a few species of gomphine dragonfly nymphs shows that there are three pairs of small intersegmental sclerites: a median pair (the members of which are narrowly separated from one another), a lateral pair bearing the spiracles, and a ventrolateral pair anterior to the katepisternum. Some, if not all, of these plates are referred to as prothoracic spiracle plates by Snodgrass (1909) who states that "in the adult they unite with each other across the back, thus forming a complete spiracular dorsum which fuses with the mesothorax..."

The katepisternum (KEP_2) is a vertical sclerite ventrally separated from the sternum by a distinct oblique suture, the sternopleural suture (SPS), from which two large apodemes, the prefurca (PF_2) and the squame (TN_2), are produced internally. Anteriorly the katepisternum is flanged by a narrow strip of sclerite which is continuous with the mesosternum and is probably a part of it.

The mesepimeron (EPM_2) is fused with the metathoracic anepisternum, except below the metastigma where the middle lateral suture (MLS), is separated from the mesepimeron.

This sclerite surrounds the posterior half of the meso-thoracic coxal cavity.

The metathoracic episternum is divided into two parts, the anepisternum (AES_3) and the katepisternum (KEP_3), by an incomplete and slightly undulate suture below the meta-stigma. Dorsally the anepisternum is produced into a hairy lobe between the two wing bases. Ventrally the katepisternum extends to a place lateral to the furcal pit, without any suture separating it from the sternum. The metathoracic epimera (EPM_3) are very large fusing ven-trally with each other to make a large unsutured area. This area bears a conspicuous median inverted Y-shaped pigmented area that is quite in contrast to that of the neighboring regions because of its lighter cclor and the direction of pigment streaking. The Y-shaped area has longitudinal streaks while the neighboring portions have transverse streaks. A pair of small apodemes at the center of the Y and a low ridge along the stem of the Y are produced internally; the latter thickening is visible externally and was often mistakenly regarded as a suture by earlier workers. The area between the arms of the Y is called poststernum or pseudosternum (PSTN) and is gen-erally regarded as a secondary sclerite filling the gap between the metasternum and the first abdominal sternite.

This interpretation seems very inadequate and a more careful study of this sclerite is very desirable. The postcoxale (PCX_3) is situated on the mesal edge of the metathoracic coxal cavity. The latter is elongated, with the coxal articulatory process lateroposteriorly located.

Sterna (Fig. 24)

The mesosternum (IIST) is a clearly defined area between and in front of the two furcal pits, medially keeled, laterally separated from the katepisternum by an oblique suture, the sternopleural suture (SPS), anterolaterally produced into a narrow piece along the anterior margin of the katepisternum on each side. The furcal pits (FP_2), or apophyseal pits (Ferris, 1940), are close to one another, and are situated near the mesal margins of the coxal cavities. The metasternum (IIIST) is medially keeled, laterally deeply invaginated along both sides of the keel (Fig. 26, posterior view of cross section of metasternum posterior to furcal pits; Fig. 27, anterior view of cross section of same slightly posterior to the preceding section), and partly obscured by the approximately raised postcoxales (PCX_3).

Synthoracic Endoskeleton (Fig. 25)

The synthoracic endoskeletal projections are of different forms: (1) ridges, (2) a complicated fusion product called the neural canal surrounding the nerve trunk, and (3) a median horn-like apodeme on the spiracular dorsum.

The ridge-like apodemes are meso- and metapleural, intersegmental, peristigmatic, and precostal apodemes. The meso- and metapleural apodemes (PLA_2, PLA_3) are strengthened by about eight short ridges projecting from their posterior sides. The lower portion of the mesopleural apodeme along the edge of the katepisternum and the apodeme between the an- and katepisternum are inappropriately called (due to different interpretation of sclerites) the sternoepimeral and sternoepisternal apodemes respectively by Tillyard (1917). The intersegmental , or interpleural apodeme (IPLA) is a simple ridge with a spine-like process at its upper end near the metastigma, and with a very long fine tendon projecting from it at about the middle of its course. The peristigmatic apodeme (PSA) lies along the suture separating the metathoracic an- from the katepisternum. The precostal apodemes are situated along the mesothoracic sternopleural sutures. From each precostal apodeme two

distinct structures are produced: the prefurca (PF_2) and the squame (TN_1). The prefurca is a tougue-like structure along the edge of the stigmatic lamina. The squame (which term is also used in maxilla) consists of a short stalk apically expanded into an elongate flat surface, situated anterior to the coxal cavity: this is regarded by Tillyard, probably erroneously, as a part of the furca.

The neural canal (Figs. 26, 27: NC) is a complicated fusion product of several invaginated processes. This fusion product is differentiated into two portions: an anterior portion on the mesosternum and a posterior portion on the metasternum. These two portions are connected dorsally, but are open between them on each side.

The anterior portion of the neural canal is formed into a complete ring by the apical fusion of the mesothoracic furcal arms. The dorsal portion of this ring-like structure is expanded into a flat surface which is produced anteriorly into a pair of short protuberances, a pointed process curling ventrad (Fig. 24), and lateroposteriorly into a long flat arm which is attached to the posterior margin of the postcoxale to act as a brace.

The posterior portion of the neural canal is an elongated structure formed by the apical fusion of the invaginated sternal fold (Fig. 26, PLF). The dorsal

of this fusion product is greatly expanded into a shield-like structure which is an elongate, ovoid, flat surface, with two foci of heavy sclerotization anteriorly and posteriorly with a pair of long narrow ribbon-like tendons (Fig. 25). The foci of sclerotization indicate the positions of the metathoracic furcal arms which are lateral to the sternal folds (Fig. 25). From each focus a very long fine tendon is produced.

Wings

The wings are held horizontally on both sides of the body: they are unable to fold back on the top of the abdomen. This method of holding the wings is pointed out by Crampton (1924) and his contemporary workers as an important archaic characteristic of the Palaeopterygota (including as living forms the dragonflies and mayflies). It appears that this condition is accounted for by the primitive structure of the wing base. However, it is interesting to note that great confusion exists in the literature regarding the structure of the regions at the bases of the wings of dragonflies and possibly also of mayflies. Structures involved are (1) wing base, (2)

axillary sclerite and lateral regions of scutum, (3) pleural wing process and epipleurites, (4) principal wing muscles, (5) articulatory points, and (6) the mechanics of flight.

Wing base -- The wing base (fused bases of wing veins) consists of two strongly sclerotized plates, the anterior humeral plate (HP) and the posterior axillary plate (AXP). Dorsally the humeral plate is divided into three lobes by transverse grooves. Ventrally the lateral edge of the humeral plate is connected by membrane to the distal margin of the pleural wing process. It does not seem to form an articulation with the anterior arm of the pleural wing process such as is mentioned by Snodgrass (1935, p. 221). The axillary plate is subquadrate in shape, slightly convex dorsally, posteriorly fused with the axillary cord (AXC). The costal vein (C) is articulated with a small intermediary plate (IP) which is in turn articulated with the posterior lobe of the humeral plate. Ventrally a short rounded protuberance is found at the fused bases of C and Sc. The veins posterior to R+M are firmly fused with the axillary plate. The base of R+M is forked. Its dorsal branch strengthens the anterior margin of the axillary plate. Its ventral

branch forms a process which is articulated with the pleural wing process and is connected with the subalare by tough membrane. Thus the base of R+M has the same function as the second axillary of other orders of insects. It is probable that the second axillary sclerite is formed by detachment of a portion of the base of R+M or R.

Axillary sclerite -- Regarding the axillary sclerite(s), special attention is given to (1) the number and (2) the origin, since there appears to be a considerable amount of confusion in the literature regarding these considerations. In the species studied here there is only one, i.e., the first axillary sclerite (1AX) described previously. This sclerite has the same shape and is situated at the same position as that illustrated by Snodgrass (1909) for Pachydiplax longipennis. Another small sclerite between the adnotal sclerite and the anteromesal margin of the axillary plate is probably detached from the adnotal sclerite. Its homology is not certain.

Crampton (1924) mentioned that in Palaeopterygota "there are frequently no alar ossicles, or at most but one." Forbes (1943) maintained that in the dragonflies there are no basal sclerites dorsally, or "no trace of dorsal axil-

lary sclerites as separate elements." Snodgrass (1909) pointed out that "only one distinct axillary is present" in the dragonflies. This axillary sclerite is clearly illustrated by him in his earlier paper (1909, Fig. 17, 1Ax), but not mentioned nor illustrated in his later paper (1938) or his well-known "Principles of Insect Morphology" (1935). The present studies are in agreement with Snodgrass but not with Forbes.

As to the origin of the axillary sclerites, Crampton and Forbes differ in opinion. Forbes (1943) mentioned that "the extreme bases of the veins are modified into a series of thickened knobs, the axillary sclerites." Crampton (1942) maintained that "the axillary sclerites, alar ossicles or pteralia, ... are apparently formed, in part, as detached portions of the lateral region of the notum, and partly as detached basal portions of the wing veins, or as sclerotized areas at the bases of the veins." He considered, on the basis of numerous comparative studies, that the first axillary or the notopterale (notale) "probably represents a detached portion of the lateral edge of the notum." Crampton's opinion is adopted in this paper since in Anax junius the condition of fusion of the first axillary with the anterior

notal wing process is perhaps indicative of such an origin.

Pleural wing process and epipleurites -- At the dorsal end of each pleural suture the pleuron is produced into an inverted foot-shaped pleural wing process (PLP). The tip of the foot (the posterior longer arm of the wing process) acts as the principal pivot for the articulation of the wing. The heel of the foot (the anterior shorter arm of the process) is connected to the humeral plate by membrane and does not seem to form an articulation with the latter. The anterior basalare (BA) and the posterior subalare (SA), collectively called the epipleural sclerites or paraptera, are present. They are very small externally and so deeply imbedded in the membrane as to be easily overlooked. Internally each has a very large apodeme which has a stalk greatly expanded apically into a large surface for the attachment of the depressor muscle. The basalare is connected by tough fibrous membrane to the lateral portion of the anterior lobe and, to a lesser extent, to the posterior lobe of the humeral plate. The subalare is connected by similar membrane to the ventral branch of the base of R+M. It is also interesting to point out that the presence of the basalare and the sub-

alare in dragonflies was probably correctly determined for the first time by Forbes (1943). They were considered as "cap-tendons" by earlier workers (Calvert, 1893; Tillyard, 1917). Snodgrass (1935) mentioned that "there are no epipleural sclerites in the dragonflies." Probably he also considered the epipleural sclerites as tendons, since in the same works he mentioned that "in Odonata there are two anterior wing muscles ....inserted by long tendon directly on the large humeral plate of the wing base", and that "two posterior pleural wing muscles take their origins on the ventral edge of the epimeron in each alate segment and are inserted directly on the axillary plate of the wing base." However, they seem to be more appropriately considered as basalare and subalare instead of tendons, since (1) they are distinct, though small, sclerites imbedded in the membrane in the same positions in which the epipleurites are found in other orders of insects; (2) they serve for the attachment of direct muscles as they also do in other winged insects; and (3) they are connected to the wing base by tough membrane as in other winged insects. Particular attention is called to the connection between the subalare and the ventral branch of the fused bases of R+M -- a condition similar to the connection between the

subalare and the second axillary sclerite.

Wing muscles -- Nine wing muscles in dragonflies have been recognised by Berlèse (1909), Calvert (1893), and Tillyard (1917), but the apodemes of some sclerites to which the muscles are attached were called cap-tendons, and the sclerites considered to be of no morphological importance. Of the nine muscles, three are very large: (1) the principal elevator, (2) the anterior depressor, and (3) the posterior depressor. The principal elevator (see Tillyard, 1917, p. 204, fig. 89, A, pe_1 and pe_2) is attached to the great apodeme (AP_2, AP_3) produced internally from the detached plate of the scutum. The anterior and posterior depressors are attached to the basalare and subalare respectively.

Snodgrass (1935) classifies flight muscles into two types, direct and indirect. The direct muscles are the axillary and epipleural muscles and the indirect are the dorsal and tergosternal muscles. The tergosternal muscles, according to Snodgrass, "are attached dorsally on the anterior lateral areas of the tergum, and ventrally on the basisternum before coxae." The present study shows, however, that dragonflies have both types of flight muscles. This interpretation differs from what Forbes

(1943) states that in Odonata the indirect muscles are "non-functional" or that "only direct wing muscles" are present. The direct (epipleural) muscles have been discussed before. There are several pairs of indirect muscles the most important of which are the principal elevator muscles, which are attached to the detached portions of the scutum dorsally and to the "squame of furca" (produced internally from the pleurosternal sutures) ventrally. They have been homologized with the "first tergosternal" of other insects by Berlèse (1909) whose opinion is adopted by Tillyard (1917). The dragonfly wing mechanics appears therefore to be not fundamentally different from that of higher groups of insects.

Articulatory points -- Each wing is articulated with the thorax in three places: (1) The ventral branch of R+M articulates with the posterior arm of the pleural wing process. This is the principal pivot of the wing. (2) The humeral plate articulates with the prealare. (3) The axillary plate articulates with the posterior notal wing process. The prealare-humeral articulation is particularly interesting in two respects: First, the prealare normally "extends laterad or ventrad to the episternum and thus supports the notum anteriorly on the pleural wall of the

segment! (Snodgrass, 1935) In the present species, the prealare is separated from the episternum by a large membranous region. It does not offer any support to the notum anteriorly; the latter is subjected to move up and down freely and synchronously with the movement of the wings. Secondly, the prealare-humeral articulation is probably unique to dragonflies, since in other winged insects the wings are articulated with the anterior wing processes instead of the prealares.

Mechanics of flight -- Since the author has not studied the muscles involved in controling the wing movements, a discussion on the possible mechanics is based on inferences concerned with the sclerotized structures described on the previous pages.

The wing mechanics in the dragonflies are similar to those of higher winged insects in two fundamental respects: (1) The wings are primarily controlled by the antagonistic indirect elevator muscles and the direct depressor muscles attached to the detached lateral plates of scutum and epipleurites respectively; (2) the subalare is connected to the wing base very close to the fulcrum while the basalare is far in front. This latter condition indicates that a pull upon the posterior depressor muscles would

strongly depress the wing while a pull upon the anterior depressor not only would depress the wing but also deflect the anterior part of the wing to produce the sculling type of flight.

On the other hand, the wing mechanics in dragonflies differs from those of higher winged insects in two important respects: (1) The prealare-humeral articulation is probably unique in dragonflies. This articulation forms the anterior part of the hinge line and differs from that in other winged insects in which the anterior notal process forms an important articulatory point. (2) Probably also unique to dragonflies are that the terga are connected to the pleura by membrane only and that the phragmata produced internally along the antecostal sutures are very small. The latter fact indicates that the longitudinal dorsal muscles attached to the phragmata would be small, such as illustrated by Berlèse (see Tillyard, 1917, p. 204, fig. 89, A, pt). The small size of the dorsal muscles probably indicates that they do not produce an effective antagonistic action to the tergosternal elevator muscles. Judging from the above facts, it seems that the terga must probably move up and down during flight without distortion. This condition differs from that of other winged insects in which

"the restoration of the dorsal curvation of the back by the contraction of the longitudinal dorsal muscles" will effect, in part, the downstroke of the wings (Snodgrass, 1935, p. 234).

As to the control of the direction of flight the fore wings are probably more important in this action than the hind ones. This contention is based on the fact that the articulatory plates of the scutum are distinctly separated from the main body of scutum (detached plates) in the mesothorax but firmly fused with it in the metathorax. Thus the hinge line and consequently the pitch of the forewing can be changed but that of the hind wing appears to be fixed.

Wing venation (Figs. 31, 32)

The wings are transparent and supported by numerous veins forming a complicated network. The fore wings (Fig. 31) are widest at the nodus (N) which is located at the middle of the anterior margin of the wing. The hind wings (Fig. 32) are slightly shorter and about one-fifth again as wide as the fore wings (the widest portion of the former is a little basal to the nodus which is situated at the basal two-fifths of the wing). In the

male the inner margin of the hind wing is excavated and fringed with a narrow white edge, the membranule (mb), and the anal angle, or tornus (Aa), angulated. In the female the inner margin of the hind wing is not excavated and the anal angle is rounded.

Both pairs of wings have a very conspicuous pterostigma (Pt) of the same size, shape and color. The pterostigma is also called stigma or anastomosis, the latter being very rarely used. The term stigma, though frequently used, is rather confusing because it may refer also to the spiracle. It is a thickendd area between Sc (Fraser, 1948) and R_1 near the apex of the wing, dark brown or black in color, elongate, about four times as long as wide, with its two shorter sides oblique and parallel to each other; with its longer sides concave, surmounting about six cells; and with a strong vein, the brace vein (br. v.), extending down from its basal side.

Several systems of notations of the venation have been proposed. Originally, de Selys gave a name to each vein without notation in use. Later on, Needham gave an interpretation based on the larval wing tracheation, with a notation based on the Comstock-Needham system. This system has been widely used in the last thirty years or so.

Tillyard (1926) gave a different interpretation, based on the study of fossil forms. His system with a few modifications has been generally accepted by later entomologists. Borror (1945) summarized in two tables the different systems of terminologies used by different authorities, such as Selys, Kirby, Needham, Tillyard, Tillyard and Fraser, and others. Forbes (1943) gave very different notations. Fraser (1948) modified the costal vein and the anal veins. The present paper uses Tillyard's system (1926) with a few modifications by subsequent workers. To summarize the points, a table is prepared to show a comparison of terminology of the principal longitudinal veins of the dragonfly wing.

Table I. Comparison of Terminology of Odonate Wing Venation
The Principal Longitudinal Veins

Terminology used in this paper		Selysian system	Needham (1903)	Tillyard (1917)	Tillyard (1926)	Tillyard & Fraser (1938)	Forbes (1943)
Name	Abbrev-iation						
Costa + Subcosta	C + Sc	Costa	CC	C	C	C	C
Subcosta	Sc	Subcosta	Sc	Sc	Sc	Sc	Sc
Radius + Media (Wing base to arculus)	R + M	Median	R + M	R + M	R + M	R + M	R_1 Rs+M+Cu
First Radius	R_1		R_1	R_1	R_1	R_1	R_1
Radial sector	R_{2+3}	Upper sector of arculus	M_{1+2}	M_{1+2}		Rs	
Second Radius	R_2	Principal Sector	M_1	M_1	R_2	R_2	R_2
Second Radius Intercalary	IR_2	Postnodal Sector	M_{1a}		IR_2	IR_2	
Third Radius	R_3	Nodal Sector	M_2	M_2	R_3	R_3	R_3
Third Radius Intercalary	IR_3	Subnodal Sector	Rs	Rs	IR_3	IR_3	R_4
Fourth + Fifth Radius	R_{4+5}	Median Sector	M_3	M_3	R_{4+5}	R_{4+5}	M
Anterior Media	MA	Lower Sector of arculus	M_4	M_4	MA	MA	Cu_1
Posterior Cubitus	CuP	Superior Sector of triangle	Cu_1	Cu_1	Cu_2	Cu_2	P_1
Anal	A	Postcosta	A	A_1		A'	
First Anal	A_1	Inferior Sector of triangle	Cu_2	Cu_2		1A	1Ax
Second Anal	A_2	Proximal sub-basal Sector	A_2	A_2			3Ax

Principal longitudinal veins -- The principal longitudinal veins are Costa, Subcosta, Radius (4 branches with 2 intercalaries), Media (a single vein), Posterior Cubitus, and Anal veins.

The Costa (C), or costal vein, is a simple and strong vein which, according to Fraser (1948), extends from the base of the wing to the nodus.

The Subcosta (Sc) is a long vein posterior to the Costa. According to Fraser (1948), its course is from the base of the wing to the nodus where it makes a distinct curve anteriorwards towards the costal margin, at which level it straightens out again along the margin of the apical half of the wing.

The Radius and Media have a common stem (R+M) which forms the anterior border of a large cell, the basal space (bs), at the base of the wing. From the anterior external angle of the basal space the R+M gives off two branches, namely R_1 and the anterior portion of the arculus (arc). R_1 extends to the apex of the wing. It is parallel to Sc and forms the posterior border of the pterostigma (Pt). The arculus is an oblique vein between R+M and CuP. It forms the external border of the basal space. It consists of two portions, namely the anterior portion and the post-

erior portion. The anterior portion is the fusion of the Radial sector and Media (Rs+M). They separate from the middle of the arculus. Rs is then called the superior or anterior sector of arculus and Media the inferior or posterior sector of arculus. The Radial sector has three branches, with two intercalary veins between them. The three branches are R_2, R_3, and R_{4+5}. The two intercalary veins are IR_2 and IR_3, the former being posterior to R_2 and the latter to R_3. Near the base of R_3 there is an oblique vein (O) (=LO, lestine oblique vein of Fraser, 1944) between R_3 and IR_3. The basal portion of IR_3 from its base to the oblique vein is called bridge or bridge-vein (br) by Needham. This bridge was regarded by Needham as a secondary extension of Rs backwards towards the base of the wing. Tillyard (1922) believed that "it was never formed backwards as a bridge vein but was always the basal portion of a strongly formed main longitudinal vein arising from R_{4+5} or sometimes from R_{2+3} as in most recent forms." On the other hand, Fraser (1944) regarded that "IR_3 never originated from a basal source but extended inwards from a peripherial one."

The Media (MA) is a simple vein extending from the arculus to the apical third or fourth of the posterior

margin of the wing. It is called by Lameere (1922) and Tillyard (1926) as Anterior Median (MA). Its basal portion forms the anterior border of the hypertriangle (h).

The Posterior Cubitus (CuP) is a crooked vein. It extends from the base of the wing to a point beyond the arculus and then bends abruptly posteriorly almost at right angle forming the common side of the triangle (t) and the subtriangle (s). From the posterior apex of the triangle CuP extends to a point slightly beyond or basal to the middle of the posterior margin of the fore and hind wings respectively. Lameere called this vein the posterior branch of Cubitus (CuP), and in this has been generally followed by subsequent authors on dragonflies (e.g., Fraser, 1940; Borror, 1945). Forbes (1943) called this vein the Plait vein (Pl) which, according to him, corresponds to the anal furrow of insects of other orders. The basal portion of this vein is regarded as the common stem of the Cubitus (Cu) by Needham (1903) and as the common stem of Cu_2+1A by Tillyard (1938).

The Anal vein (A) is slightly undulated at its basal portion. It meets with CuP at the apex of the triangle. The apical portion of the Anal vein (A_1) from the apex of the triangle to the posterior margin of the wing is parallel

to CuP in the hind wing. On the other hand, in the fore wing it is parallel to CuP for a long distance and then diverged from the latter. The notation A used in this paper refers to the vein from the base of the wing to the posterior apex of the triangle. A_1 denotes its extension. Tillyard (1926) regarded the basal portion (A) as a backwards extension of IA towards the base of the wing. He designated the portion from the posterior apex of the triangle to the cubito-anal cross vein (cu-a) as Ab (Anal bridge) and the portion between cu-a and the base of the wing as A'. Fraser (1938) demonstrates that the anal vein in the Odonata has an independent origin from the base of the wing. The present notation A=Ab+A' of Tillyard. In the hind wing the anal area is greatly expanded. There are three distinct anal veins, namely A_{1a}, A_2 and A_3. A_{1a} and A_2 become fused not far from their origins thus forming a 2-celled anal loop (AL). The vein that separates the anal loop into two cells is called the Anal Supplementary (mspl) or mid-rib (mr). Forbes (1943) used a new term "Axillary" (Ax) for the veins often called "anal" but which, according to him, are distinct from the original anal vein which is usually the Pl of his system.

Cross veins -- The more important cross veins are

as follows: nodal, subnodal, ante- and postnodal, primary antenodal, brace vein, arculus, oblique vein, and cubito-anal vein. The brace vein, arculus, and oblique vein have been mentioned before and will hot be repeated again.

The nodus, or nodal vein (N), is a thick vein situated between the costal margin and R_1. Both notations N and n have been used but the former is adopted in this paper. Their positions in the fore and hind wings have already been mentioned before. The anterior portion of the nodal vein coincides with the bending part of Sc. The extension of the nodal vein between R_1 and R_2 is called subnodus (sn). Between the costal margin and R_1 there are many cross veins; those between the base of the wing and the nodus being antenodal cross veins (Ax) and those between the nodus and the basal end of the pterostigma being postnodal cross veins (Px). The first and the fifth or sixth antenodal cross veins are thickened and are called primary antenodal cross veins (Ax_1 and Ax_2). It should be noted that Forbes (1943) used the same notation Ax for the veins which he called Axillary veins. This has been mentioned before. The number of the nodal veins varies. In systematic work the nodal index such as $\frac{13\text{-}16 \mid 16\text{-}12}{13\text{-}11 \mid 11\text{-}13}$ has been often used

and indicates the number of the ante- and postnodal cross veins in the left and right fore and hind wings respectively. The nodal indeces of ten specimens are shown as follows: $\frac{13\text{-}16 \mid 16\text{-}12}{13\text{-}11 \mid 11\text{-}13}$, ♂; $\frac{11\text{-}14 \mid 15\text{-}11}{10\text{-}11 \mid 11\text{-}11}$, ♂; $\frac{13\text{-}18 \mid 18\text{-}11}{14\text{-}13 \mid 13\text{-}14}$, ♀; $\frac{12\text{-}15 \mid 14\text{-}12}{12\text{-}10 \mid 10\text{-}12}$, ♂; $\frac{12\text{-}17 \mid 16\text{-}11}{\text{-}12 \mid 13\text{-}11}$, ♂; $\frac{12\text{-}16 \mid 19\text{-}12}{12\text{-}11 \mid 13\text{-}11}$, ♂; $\frac{12\text{-}19 \mid 18\text{-}10}{12\text{-}10 \mid 10\text{-}12}$, ♀; $\frac{13\text{-}16 \mid 15\text{-}12}{13\text{-}11 \mid 13\text{-}13}$, ♀; $\frac{12\text{-}17 \mid 16\text{-}12}{12\text{-}12 \mid 12\text{-}13}$, ♂; $\frac{13\text{-}16 \mid 18\text{-}11}{13\text{-}11 \mid 11\text{-}12}$, ♂.

The cubito-anal cross vein (cu-a) is a vein between CuP and A basal to arculus for a considerable distance. Different notations have been given to this vein, such as ac (Anal crossing, Needham), Cu_x (Tillyard, 1917), Ac (Tillyard, 1926), AC (Fraser, 1940), and cu-a (Borror, 1945); the last notation is used in this paper. The different terminologies are accounted for largely by the different interpretations of the anal vein.

Cells and special areas -- The important cells and special areas are as follows: Pteostigma, basal space, triangle, hypertriangle, subtriangle, discoidal field, basal anal area, anal loop, anal field, and anal triangle. The pterostigma (Pt) has been mentioned before and will not be considered again.

The basal space (bs) is an area at the base of the wing, bounded anteriorly, posteriorly, and apically or

externally by R+M, CuP, and arc respectively, the first two being subparallel and the last slightly slanting. It is also called by different names, such as median space, midbasal space, sub-basal space, and basilar space. It is about 3½ to 4 times as long as wide.

The triangle (t) is a distinct and almost isosceles triangular space formed by CuP basally and two cross veins anteriorly and apically (or externally) respectively. A space anterior to the triangle from arc to the apex of the triangle is called hypertriangle (h) which is also called by different names such as supratriangle, hypertrigone, or supra-trigone. It is a narrow space bounded basally by the posterior portion of the arculus or m-cu, anteriorly by a portion of MA, and posteriorly by a vein which is composite. The basal portion of this composite vein is a part of CuP and the distal portion a cross vein between CuP and MA. This cross vein is also the anterior side of the triangle. It has such direction that it looks like part of a longitudinal vein. The subtriangle (s), or internal trinalge, is also an isosceles triangle. It is situated basal to the triangles with the vertical part of CuP as their common side. It is bounded externally by the vertical part of CuP, posteriorly by a part of A, and

basally by a slanting cross vein between CuP and A. Phylogenetically the triangle and the subtriangle are collectively called the cubital area, which is homologous with the discoidal cell or quadrangle of Zygoptera. The area apical to the triangle between MA and CuP is called the discoidal field. The discoidal field in the fore wing is of almost the same width throughout except the portion beyond the level of nodus is slightly widened, while that of the hind wing is considerably widened at the posterior margin of the wing. The difference in shapes of the discoidal fields in both wings is accounted for by the different positions of the apical portion of the CuP.

The basal anal area is a narrow space posterior to the basal space. It is situated between CuP and A and is limited by the cross vein cu-a.

The anal loop (AL) is a two-celled area in the hind wing bounded by A, A_{1a} and A_2 on its anterior, apical, and basal sides respectively. It is bisected by a short vein, the anal supplementary, or mid-rib (mr).

The anal field refers to the area bounded by A, A_3, A_{1a}+A_2, and the posterior margin of the wing. It

includes the anal loop in the hind wing. In the fore wing its apical limit is about at the level of the posterior apex of the triangle. The anal field has two rows of cells between A and the posterior margin of the fore wing, whereas there are five rows in the hind wing.

The anal triangle (at) is a 4-celled space at the extreme base of the hind wing in the male, bounded anteriorly, externally and basally by A, A_3, and the basal margin of the wing respectively. The basal margin of the hind wing is flanged by a narrow whitish membrane, the membranule (mb). In the female the anal triangle is 8- or 9-celled.

Legs (Figs. 28-30)

The legs are small in comparison with the size of the body. They are strongly armed with spines. The prothoracic legs are the smallest, being slightly smaller than the mesothoracic legs which in turn are considerably smaller than the metathoracic legs. The difference in size of the legs is accounted for especially by differences in length of the femur, tibia, and tarsus since the coxa and trochanter are not conspicuously different in lengths in the three pairs of legs.

The coxa (CX) is of moderate size, more or less conical in shape, with its outer surface much longer than its inner surface which is conspicuously bulged. The basal portion of the outer surface is modified to form the pleural articular socket which is articulated with the pleural process of the thorax. The basal end of the coxa is girdled by a submarginal basicoxal suture (BCXS), along which a ridge, the basicosta, is produced internally. The basicosta is enlarged on the outer surface posterior to the pleural articular socket. The basicostal suture sets off a marginal flange, the basicoxite (BCX), which is enlarged on the outer surface posterior to the pleural articular socket. Distally the coxa bears an anterior and a posterior articular socket to which the trochanteral articular condyles are attached.

The trochanter (TR) is a slender segment, about as long as the coxa, having a short outer surface so that its distal end is obliquely truncated. A transverse constriction gives this segment a superficially 2-segmented appearance. The basal portion is attached to the coxa by an articular membrane. It is also articulated with the coxa by an anterior and a posterior trochanteral articular condyle. The coxo-trochanteral condylic hinge is

a right angle with the pleurocoxal articulation so that it there forms an "universal joint" which allows a wide range of motion of the leg. A condylic hinge is also present at the distal end of the trochanter. This operates at a right angle to the coxa-trochanteral condylic hinge, but permits of much less freedom of motion than the latter since nearly the entire basal rim of the femur is closely attached to the distal end of the trochanter.

The anterior surface of the articular membrane between the coxa and trochanter is invaginated to form a deep pouch, the posterior wall of which is thickened and tendon-like in structure. This undoubtly serve for the attachment of a muscle internally.

On the inner wall of the trochanter there is a group of short and robust spines. There are only 4 or 5 spines on the basal, and the same number on the distal, portion of the trochanter of the prothoracic leg, whereas there are many on the distal portion of the trochanter of the meso- and metathoracic legs. These spines are arranged at random: they are not arranged in a definite row to form a trochanteral brush such as reported by Cowley (1937) to occur in some other dragonflies.

The femur (FE) is the longest segment of the leg,

nearly cylindrical, armed with short stout spines on its inner surface which faces ventrally in its natural position. The front femur is slightly curved and therefore fits nicely along the side of the thorax. The hind femur is straight, slightly compressed, and is held beneath the thorax. Its spines are more irregularly arranged on the basal portion than on the distal portion where they are distributed in two distinct rows. Proceeding distalward the spines are progressively larger and more widely separated. The area between the two rows of spines is smooth, flat, or slightly grooved, fitting it for the reception of the tibia when the latter is flexed close against the femur. The distal margin of the femur is crowned with a few short spines.

The tibia (TI) is a slender segment, convex on its dorsal or outer surface, flattened on its ventral or inner surface, armed laterally with a row of flattened spurs and dorsally with two parallel rows of short spines. It is constricted and slightly bent near its basal end which is articulated with the former by an anterior and posterior condyle. The articular membrane between the femur and the tibia has the same condition of invagination as that

found in the membrane between trochanter and femur.

The flattened lateral spurs are of two types: (a) The short and sword-like type. (b) The elongate type. The short sword-like spurs are about 8 or 9 in number in a row, is situated on the apical half of the anterior margin of the prothoracic tibia in either sex. They are collectively called tibial comb (TIC) which was first pointed out by St. Quentin (1936) to be present on the prothoracic tibia of all dragonflies. Each spur is set on a socket which is oblong in shape. The spur is not evenly sclerotized with its one edge unpigmented and thinner than the other edge. The elongate type of spur is long, undulated, and pointed at the apex. Along the anterior margin of the tibia there are four such spurs basal to and one apical to the tibial comb on prothoracic leg, whereas eight on meso- or metathoracic leg where the tibial comb is absent. Along the posterior margin of the tibia there are eight to ten such spurs.. Proceeding distalward these spurs are progressively shorter but broader.

The function of the tibial comb is unknown. Garman (1917) said that it might be used for the cleaning of the mouth parts and antennae. Needham and Haywood (1929)

said that it might serve to hold the dragonflies' food. St. Quentin (1936) mentioned that it might be used for the cleaning of compound eyes.

On the ventral surface of the tibia there is a group of bristles along the base of the tibial comb and a non-sclerotized structure near the distal end of the tibia. This non-sclerotized structure is elevated and eongated. It is present on the prothoracic tibia of the male sex only. So far as my knowledge goes this special structure occurs in many species of gomphine dragonflies which I have examined. It has apparently not been reported heretofore. Its function is not obvious to me.

The distal end of the tibia is hotched and somewhat socket-like and therefore fitted for the reception of the bulbous basal region of the basitarsus.

The tarsus (TA) is 3-segmented; the basal segment or basitarsus (BTA) is the shortest; the distal segment or distitarsus (DTA) is the longest. The latter is about as long as the basitarsus and the middle segment taken together. Each segment is armed with a few spurs on its lateral margin. The distitarsus (DTA) bears a ventro-distal projection, the plantella (PTL), which is well developed.

The pretarsus (Fig. 30) or terminal region of the leg consists of a pair of claws, empodium, and unguitractor. The claws (CL) are the largest parts of the pretarsus, and they articulate with a small dorsal process of the distitarsus. Each claw bears a ventral tooth and a narrow wavy ridge-like structure on each side of it. Ventrally the bases of the claws are connected with membrane which is also closely attached to the mesally located unguitractor The unguitractor is a ventral sclerite which is partially hidden by the distal projection of the distitarsus, the plantella. An empodium (EMP) is attached to the distal end of the unguitractor. The distal portion of the empodium is enlarged.

ABDOMEN (Pls. 6-9)

The abdomen is composed of 10 distinct segments and, according to Tillyard (1917), also of the reduced remnants of the 11th and 12th segments. It is long and slender; the basal two segments tumid and slightly compressed; becoming thin, slender, and cylindrical from segment 3 to 7 (more pronouncedly so in the male); dilated and depressed from the posterior half of segment 7 to 9 (more pronouncedly so in the male), widest across the apical end of the

segment 8; segment 10 ring-like (in male) or depressed (in female). The proportional lengths of the segments from base to apex are approximately as follows: 1.8 : 4.5 ; 6.0 : 7.0 : 7.0 : 6.5 : 5.5 : 4.6 : 2.5 : 1.5

The male differs from the female in (1) having auricles (AU) on segment 2, (2) in having accessory sexual organs (Figs. 40-44) on the ventral surfaces of segments 2 and 3, (3) the relatively great dilation of the segments 7-9, and (4) the relatively great length of the anal appendages (Figs. 45-50) at the extreme apex of the abdomen.

Male -- Tergites

The tergites are convexly arched. They occupy not only the dorsal but also the whole of the lateral regions of the segments. The lateral edges of the posterior half of tergite 3 and also of tergites 4-6 almost meet mid-ventrally partially hiding the sternites from view. With the exception of segments 1 and 10, the tergites are distinctly separated from the sternites by pleural membrane. Tergites 1 and 2 are weakly sclerotized mid-dorsally; 3-7 weakened along the mid-line; and 8-10 not so weakened. Tergites 3-7 are adorned with minute spines

mid-dorsally and also along the posterior transverse and submarginal ventral carinae. The dorsal spines are absent on the tergites of the other segments. Tergites 3-6 are similar to one another, while those of the other segments differ from the former in various ways. Tergite 4, to be described first, illustrates the generalized condition.

Tergite 4 is strengthened by the formation of both internal ridges and external carinae. Basally it is girdled by a submarginal antecostal suture (ACS), which is very narrow and usually obscured by the apical portion of the preceding tergite. Dorsally the tergite is weakened along its mid-line but, conversely, is strengthened by a supplementary transverse carina (SUTC) which is situated at a point one-fourth the distance from base to apex of the segment. Posteriorly it is strengthened by the submarginal posterior transverse carina (PTC) which is continuous with the submarginal ventral carinae (SVC), one on each side along the ventral margins of the tergite. The posterior transverse carina is conspicuous and adorned with small spines. The submarginal ventral carinae are poorly formed and weakly sclerotized.

Tergite 1 is separated from the sternite by narrow pleural membranes except anteriorly where it is fused with

the latter. Dorsally it is adorned with a pair of tufts of long, fine hairs each on a slightly elevated subapical area. Lateroventrally the acrotergite (ATG) is enlarged and produced into a pouch-like evagination on each side. All carinae are absent except the submarginal ventral carinae (SVC) which are very poorly developed, with or without a few minute spines.

Tergite 2 is peculiar in having a pair of lateral outgrowths, the auricles (AU). These are situated in an oblique position on the anterior portion of the tergite, and are weakly sclerotized except along their crests which are denticulate ventrally. The supplementary transverse carina (SUTC) is situated slightly anterior to the middle of the tergite and extends downward on each side posterior to the auricle. A similar but much shorter structure is present posterior to the supplementary transverse carina. The submarginal posterior transverse carina (PTC) is more prominent dorsally than laterally. The submarginal ventral carinae (SVC) are adorned with long hairs anteriorly and with spines posteriorly.

Tergite 7 (Fig. 45) is peculiar in having the median area of the submarginal posterior transverse carina raised considerably and the submarginal ventral carinae dilated

into leaf-like structures, the pseudo-lateral dilations (PLD) (Fraser, 1934).

Tergite 8 (Fig. 45) is peculiar in having a pair of submedian, low, rounded, transversely wrinkled tubercles. The supplementary transverse carina is absent. The submarginal posterior carina is raised medially where it is deeply notched. The submarginal ventral carinae are greatly expanded to form pseudo-lateral dilations.

Tergite 9 is similar to the preceding one except that (1) it is without submedian tubercles, (2) it is submedially slightly constricted on both sides, and (3) its submarginal posterior carina is slightly notched medially.

Tergite 10 is completely fused with the sternite to form a ring. Dorsally it is deeply concave on its apical margin, with a pair of sub-basal, very low, ovoid, transversely wrinkled tubercles followed by dorsal wrinkles paralleling the edge of the apical concavity. All carinae are absent: the position of the submarginal posterior carina is indicated by a few small spines laterally.

Male -- Sternites

Sternite 1 (Fig. 40) is short, transversely rectangular,

anterolaterally fused with the tergite. Posteriorly it is produced into two short processes which are inflected and obscured from view by the main portion of the sternite. These processes are connected with the anterior processes of the anterior lamina of the sternite 2. Laterally the sternite has a pair of ovoid spiracles and a pair of small pits mesoposterior to the former. From these pits short horn-like apophyses are produced internally.

Sternite 2 and the anterior portion of the sternite 3 are greatly modified into complicated accessory sexual organs which are collectively known as the copulatory apparatus. The main structure of the apparatus consists of a penis which is lodged in a membranous depression, the genital fossa and is protected by various organs derived from sternite 2. Different parts of the apparatus will be described in detail as follows.

Sternite 2 (Figs. 40-43) is modified to form the following parts: genital fossa, anterior lamina, posterior lamina, supporting framework, sheath of the penis, anterior hamules, and posterior hamules.

The genital fossa (GF) is a membranous depression strengthened by anterior lamina, posterior lamina, and lateral supporting frameworks. The sheath of the penis (SHP) is located on the posterior part of this membrane.

The anterior lamina (AL) is a large sclerite, situated at the anterior third of the second abdominal segment. It is differentiated into distinct anterior and posterior portions. The anterior portion is flat, comparatively weakly sclerotized, anteriorly produced into two processes which are connected with similar processes of the preceding sternite. The posterior portion of the anterior lamina is strongly sclerotized, convex, and adorned with many minute tubercles and hairs. The posterior margin of the anterior lamina is V-shaped, irregularly indented, and with a short median cleft, the cleft of the anterior lamina (CAL).

The posterior lamina (PL) is a large sclerite situated at the posterior end of the second abdominal segment. It is weakly sclerotized, constricted medially, and greatly expanded laterally.

The supporting frameworks, or the anterior portions of the frameworks (APF) (Thompson, 1908) are a pair of sclerites on the lateral sides of the genital fossa between the anterior and the posterior laminae. Each is an elongate sclerite, slightly convex ventrally, with a subapical mesodorsal process which supports the base of the sheath of the penis (SHP). Ventrally the sclerite has a low transverse

ridge to which the posterior margin of the base of the anterior hamule (AH) is attached. Posteriorly the sclerite is emarginated to form together with the anterior extension of the posterior lamina (PL) a socket to which the posterior hamule (PH) is attached.

The sheath of the penis (SHP) is a placoid structure composed of a scoop-like structure arising ventrally from the base which is imbedded in the membranous genital fossa. The scoop is supposed to be for the protection of the penis. The base of the sheath is five-sided, medially with a broad shallow groove. The anterior margin of the base is articulated with and supported by the two arms of the paired supporting frameworks. Each of the posterolateral angles of the base is connected with a small slender sclerite, the outer end of which is articulated with the posterior margin of the base of the posterior hamule.

The anterior hamules (AH) each consists of a long bifurcated process produced ventrally from the posterior portion of an elongate sclerite which is attached to the low ridge of the supporting framework. Mesally it is attached to the lateral margin of the anterior lamina. The two processes are of unequal length, pointed apically. The anterior process is hooked apically, about twice as long as

the posterior process, and is subequal in length to the stem.

Each of the posterior hamules (PH) is a robust structure attached to the socket formed by the supporting framework and the posterior lamina. It is about as long as the anterior hamule, pointed, with more bristles on its mesal surface and apex than elsewhere.

Sternite 3 is modified anteriorly into a penis and posteriorly into a long, narrow sclerite; the former is abutted to the truncated end of the latter. Anteriorly the narrow sclerite bears a large, round, internal apodeme on each side.

The penis (Fig. 44) is a complicated organ consisting of several segments. Different designations for each of the segments of the penis of anisopterous dragonflies have been proposed by various taxonomists. A table is here given to show the different terminologies. Those terms used by Fraser (1940) in his paper on the penes of a large number of gomphine dragonflies are adopted in the present paper with a few modifications.

Authors	Williamson (1920)	Kennedy (1922)	Borror (1942)	Fraser (1940)	Present author
Dragonflies studied	Desmogomphus	Libellula	Erythrodiplax	Gomphidae	Onychogomphus ardens
Segments	Vesicle	Segment 1	First or basal segment	Vesicle	Vesicle
	Segment 1	Segment 2	Second segment	Stem or First joint	Stem
	Segment 2	Segment 3	Third segment		
			Fourth or Terminal segment	Median or Second joint	Median segment
	Segment 3	(Elongation of distal meatus of segment 3)		Glans or Distal joint	Distal segment

The vesicle (VS) is a robust structure, heavily sclerotized except for its dorsal surface which is membranous, having a small sclerite imbedded in its posterior portion. This sclerite is connected to the posterior extensions of the posterior lamina by a pair of small sclerites. These slender sclerite apparently have not been recorded in the literature. When viewed ventrally (Fig. 40) the vesicle is slightly constricted near the base, widened apically, slightly protruded on its apical angles, and with a short median cleft. The cavity of the vesicle is filled with fluid, and is continuous with those of the succeeding segments of the penis, but not with the haemocoele of the abdomen. The latter fact is contrary to the opinion maintained by Kennedy (1922) and probably also by Borror (1942).

The vesicle is an important organ in relation to the erection of the penis, but the exact role that it plays remains obscure. Kennedy (1922) mentioned that the cavity of the vesicle is continuous with the haemocoele of the abdomen, and that the erection of the penis is accomplished by forcing blood from the latter through the vesicle to the cavity in the apical segments of the penis. This opinion is adopted by Borror (1942) with modification.

Fraser (1940) says that "when pressure is raised in the vesicle .... the penis" is "at once erected." But he does not mention how the pressure is raised in the vesicle. From the present studies it appears that the raising of pressure in the vesicle is accomplished by exerting a force on the small sclerite imbedded in the dorsal membrane of the vesicle. This contention is based on the observation that the cavity of the vesicle is not continuous with the haemocoele and that the wall of the vesicle is rigid except for the dorsal surface which is membranous. Thus a force exerted on the small sclerite imbedded in the membrane will depress the latter and force the fluid in the vesicle to flow into the apical segments so that the penis is erected.

The stem (STEM) is L shaped, attached to the dorsal membrane at the anterior end of the vesicle. Apically it bears a large round membrane which has a long narrow opening, the proximal meatus (PXM). The presence of this proximal meatus probably indicates that the stem is a composite segment, i.e., consisting of the second and the third segments of Borror (1942) fused together. This contention is based on the fact that (1) in Erythrodiplax and Libellula the proximal meatus is always present in a

small and distinct segment, i.e., the third segment of Borror, and that (2) the apical limit of the preceding segment is indicated by the presence of a short dorsal spur (Kennedy, 1922), or knob-like protuberance (Borror, 1942). In gomphine dragonflies this spur is absent in many species, such as shown by Fraser (1940), but present in some other species, e.g., Gomphus agricola, G. suzukii, Onychogomphus flexuosus, O. circularis, Megalogomphus hannyngtoni, Progomphus pygmaeus, Cyclophylla signata, and Stylogomphus inglisi. The latter fact indicates the distal limit of a segment proximal to the segment bearing the proximal meatus. The suture between these two segments is generally obliterated in gomphine dragonflies.

The median segment (MS) is short, perpendicular to the basal segment, and distally inflated. The inflated portion is weakly sclerotized and bears a large lobe, the posterior lobe (PLB) (Kennedy, 1922; Borror, 1942), also called preputial fold or prepuse (Fraser, 1940). Anteriorly the median segment is medially grooved. Dorsally it bears a pair of very heavily sclerotized structures to which the bilobed distal segment (DS) is attached.

The distal segment (DS), or glans (Fraser, 1940), is bilobed. Each lobe bears a curled flagellum (Fraser,

1940) or cornua (CN) (Kennedy, 1922). The distal meatus is situated deeply between the two lobes.

Sternites 4 and 5 (see Fig. 38, sternite V, ♀) are elongate sclerites. Each is differentiated into an anterior subquadrate area followed by a long narrow piece which is slightly constricted near the apex and ending in a small piece, the sternellum (STN) (Tillyard, 1917). Anteriorly the subquadrate area is produced into a pair of short processes. At the four angles of the subquadrate area, the sternite is produced internally and laterally into two pairs of sternal processes (STP) for the attachment of the segmental muscles. The anterior pair is small and linear and the posterior pair is fairly large and scale-like.

Sternite 6 (Fig. 35) is similar to the preceding sternite except that its sternellum is enlarged apically.

Sternite 7 (Fig. 35) is peculiar in that the anterior pair of sternal processes is very small, and that the long piece following the subquadrate area is widened apically; without sternellum.

Sternite 8 (Fig. 46) is a large sclerite, subtrapezoidal in shape, basally with a low median keel, and laterally slightly sinuate.

Sternite 9 (Fig. 46) is sclerotized on its basal half and very weakly so on its apical half. The sclerotized portion is 4-lobed, two on each side of a pair of median ovoid sclerites, the valvules (VV), which, according to Tillyard (1917), are homologous with the lateral processes of the ovipositor of the female. The valvules cover the male genital pore; the latter is guarded by a sclerotized ring.

Sternite 10 (Fig. 46) is fused with the corresponding tergite. Its posterior margin is deeply emarginated.

Spiracles

There are eight pairs of abdominal spiracles (SP). The first pair is situated in the first sternite described previously. The next six pairs are situated in the pleural membranes near the posterior sternal processes in each of the abdominal segments 2 to 7. They are ovoid in shape and oblique in position. The eighth pair is situated on the pleural membrane close to the middle of the lateral margins of the eighth sternite. It is almost twice as large as the other spiracles, elongate ovoid, and parallel to the long axis of the body.

Female -- Tergites and Sternites

The tergites of the female are fundamentally the same as those of the male, except for some sexual dimorphic characters mentioned before. Tergite 10 (Fig. 48) differs from that of the male in that dorsally it is not wrinkled nor tuberculate, and apically it forms a straight line instead of being deeply concave.

Of the sternites, the first, fourth, fifth, and sixth are the same as in the males. Sternite 2 (Fig. 36) differs from the more generalized condition of the above in that it is rather wide, with the anterior transverse area bearing a pair of lateral sternal process only. Sternite 3 (Fig. 37) is similar to the generalized sternite except that the anterior and lateral processes are comparatively longer. Sternite 7 (Figs. 39, 47) is comparatively broad, with very small sternellum. Sternite 8 (Fig. 47) is large, elongate rectangular, laterally sinuate, basally with a low median keel, subapically with a low protuberance, and apically with a pair of subgenital plates (SGP) which are about two-fifths as long as sternite 9. The two sclerites of the subgenital plates are called valves (or vulvar

scales, anterior processes) of the ovipositor, probably synonymous with some other terms such as ventral valves and first valvulae. Sternite 9 (Fig. 47) is broad, basally emarginate and separated from the preceding sternite by a large semicircular membrane. The female genital pore is situated in this membrane and is covered by the subgenital plates. At a point one-third the distance from apex to base of the segment a low arc-shaped ridge is produced, which is apically bordered by a narrow membrane; the latter is constricted in the middle. This ridge might possible be the remnant of the median process of the ovipositor (Tillyard, 1917) (also called inner valves or second valvulae). Sternite 10 is transversely rectangular, apically not emarginated as in the male.

End-segments

The end-segments, as used by Tillyard (1917), consist of various structures apical to the segment 10. These structures differ morphologically and phylogenetically in different suborders and in the two sexes. The following table shows their homologies (modified from Tillyard, 1917).

Segment	Name of parts	Male	Female
10	Tergite	(Present)	(Presnet)
	Sternite	(Present)	(Present)
	Cercoids	Superior anal appendages	Anal appendages
11	Tergite	Rudimentary	Median dorsal appendage
	Sternite (bipartite)	Fairly large	Fairly large
	Appendix dorsalis	Inferior anal appendages	Absent
	Circi	Absent	Absent
12	Tergite	Rudimentary	Rudimentary
	Sternite (two laminae anales)	Rudimentary	Rudimentary

In the male the superior and inferior anal appendages are very well developed. The superior anal appendages (SAP) are elongate, more than double the length of the segment 10, declined in their apical halves, slightly sinuate in dorsal view, and ventrally serrate at the apices. The

inferior anal appendage (IAP) is a bifid structure with its two branches slightly longer than the superior anal appendages. Its base bends down vertically for a short distance and bears two apposing arms which curve upward gently toward their rather acute apices. Each branch of the inferior appendage has a minute dorsal subapical tooth and a fairly large, low, internal ridge-like tubercle just opposite the apex of the superior appendage; the tubercle being adorned with fine hairs. The remnants of the 11th sternite (Figs. 46, 50) is divided into two fairly large sclerites, collectively called the bipartite 11th sternite, situated along the ventral and lateral margins of the segment 10. The 12th tergite and sternite are represented by superior and inferior anal laminae. Both are weakly sclerotized and adorned with minute hairs. The superior anal lamina (SPL) is attached to the anterior surface of the base of the inferior anal appendage. The inferior anal laminae (IFL) consist of two pieces, one attached to each of the bipartite sternite. The anal opening is situated at the bases of the anal laminae.

In the female the end-segments are comparatively short, consisting of anal appendages, median dorsal appendage, and the remnants of the 11th and 12th segments. The anal

appendages (AAP) are a pair of slender conical structures, situated laterally above the dorsal appendage, slightly longer than the 10th tergite. The median dorsal appendage, or supra-anal plate (SPP), is a sub-semicircular sclerite, convex above, about half as long as the anal appendages. The bipartite 11th sternite (Fig. 47) consists of a pair of fairly large sclerites which, when viewed ventrally, are triangular in shape. The remnants of the 12th tergite and sternite are represented by superior and inferior anal laminae. The former is weakly sclerotized, attached to the ventral surface of the median dorsal appendage. The inferior anal laminae (IFL) are bipartite, attached to the 11th sternite, and exceed the length of the latter.

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ABBREVIATIONS

Aa - Tornus

AAP - Anal appendage

AAR - Anterior mandibular articulation

AAS - Anealar sinus

AB - Anterior lobe of prothorax

ACL - Anteclypeus

ACS - Antecostal suture

AES_2, AES_3 - Meso- or metathoracic anepisternum

AH - Anterior hamule

AL - Anterior lamina

AN - Admotal sclerite

AP_2, AP_3 - Apodeme of detached plate of meso- or metathoracic scutum

APF - Anterior portion of framework

ARB - Anterior rib of anterior tentorial arm

arc - Arculus

ARG - Antealar ridge

at - Anal triangle

ATA - Anterior tentorial arm

ATG - Acrotergite

AU - Auricle

AWP - Anterior wing process

Ax_1, Ax_2 - Primary antecostal cross veins

1AX - First axillary sclerite

AXC - Axillary cord

AXP - Axillary plate

BA - Basalare

BCD - Basicardo

BCX - Basicoxite

BCX3 - Basicostal suture

BU - Brush

BPL - Basal plate

br - Bridge vein

br.v. - Brace vein

bs - Basal space

BS - Basisternum

BTA - Basitarsus

C - Costal vein

CAC - Cleft of anterior lamina

CAR - Posterior mandibular articulation

CEP - Cephaliger

CL - Claw

CN - Cornua

COL - Collar

CT - Corporotentorium

cu-a - Cubito-anal cross vein

CuP - Posterior cubitus

CX - Coxa

CXC - Coxal cavity

DC - Dorsal cervical sclerite

DCD - Disticardo

DCR - Dorsal carina

DS - Distal segment of penis

DTA - Dorsal tentorial arm

DTTA - Distitarsus

DTP - Dorsal tentorial pit

EC - Eucervicale

EH - End hook

EMP - Empodium

EPM - Epimeron

EPX - Epipharynx

ES - Episternum

ESR - Epistomal ridge

ESS - Epistomal suture

EYE - Compound eye

F - Furca

FE - Femur

FL - Flagellum of antenna

FM - Foramen magnum

FP - Furcal pit

FR - Frons

FS - Furcasternum

FT - Flexor tendon of mandible

G - Gena

GF - Genital fossa

h - Hypertriangle

HM - Hypostoma

HMS - Hypostomal suture

HP - Humeral plate

IAP - Inferior anal appendage

ICS - Incisors

IPL - Inferior anal lamina

IL - Inner lobe

IP - Intermediary piece

IPLA - Interpleural apodeme (= Intersegmental apodeme)

IR_2, IR_3 - Intercalary Radial veins

KEP - Katepisternum

LL - Lateral lobe

LR - Labrum

M - Media

MA - Anterior Median

MB - Median lobe of pronotum

mb - Membranule

MD - Mandible

MDP - Mandibular process

MH - Movable hook

ML - Middle lobe of labium

MLS - Mid-lateral suture (= Intersegmental suture)

MM - Mentum

MO - Mola

mr - Mid-rib of anal loop in hind wing

MRS - Mid-rib of anterior tentorial arm

MS - Median segment of penis

MSC - Mesostigmatic lamina

MX - Maxilla

MXP - Maxillary process

N - Nodus

NC - Neural canal

o - Oblique vein

OC - Ocellus

OCC - Occiput

OCCD - Occipital condyle

OCCH - Occipital horn

OCCM - Occipital margin

OCS - Ocular sclerite

OL - Outer lobe

OS - Ocular suture

P - Pedicel

PA - Papilla

PB - Posterior lobe of prothorax

PC - Postcervicale

PCL - Postclypeus

PCX - Postcoxale

PF_2 - Prefurca

PFS - Parafrontal suture

PFST - Postfurcasternum

PG - Postgena

PH - Posterior hamule

PL - Posterior lamina

PLA - Pleural apodeme

PLB - Posterior lobe of penis

PLD - Pseudolateral dilation

PLF - Sternal fold

PLS - Pleural suture

PM - Pleurostoma

PMS - Pleurostomal suture

POCC - Postocciput

POCS - Postoccipital suture

POS - Postocellar suture

PRA - Prealare

PRB - Posterior rib of anterior tentorial arm

PS - Parastipes

PSA - Peristigmatic apodeme

PSC - Prescutum

PSCL - Postscutellum

PSTN - Pseudosternum

Pt - Pterostigma

PTA - Posterior tentorial arm

PTAR - Pretarsus

PTC - Posterior transverse carina

PTL - Plantella

PTP - Posterior tentorial pit

PWP - Posterior wing process

PXM - Proximal meatus

R - Radius

ROOC - Rear of occiput

Rs - Radial sector

RT - Retractor tendon of mandible

S - Scape

s - Subtriangle

SA - Subalare

SAG - Subalar ridge

SAL - Salivarium

SAP - Superior anal appendage

Sc - Subcosta

SCL - Scutellum

SCS - Sternocostal suture

SCT - Scutum

SG - Sutural groove

SGP - Subgenital plate

SHP - Sheath of penis

SM - Submentum

sn - Subnodus

SP - Spiracle (ISP, IISP - Meso- and metathoracic spiracles; SP_1, SP_2, etc., - Abdominal spiracles)

SPD - Spiracular dorsum

SPL - Superior anal lamina

SPP - Supra-anal plate

SQ - Squame of labium

ST_1, ST_2, etc. -- Abdominal sternites

IST, IIST -- Meso-, metasternum

STEM - Stem of penis

STI - Stipes

STN - Sternellum

STP - Abdominal sternal process

SUTC - Supplementary transverse carina

SVC - Submarginal ventral carina

T - Tergite

t - Triangle

TA - Tarsus

TFR - Top of frons

TI - Tibia

TIC - Tibial comb

TN_1 - Squame of precostal apodeme

TR - Trochanter

UT - Unguitractor

V - Vertex

VC - Ventral cervical sclerite

VS - Vesicle

VV - Valvula

EXPLANATION OF PLATES

Plate I -- HEAD

Fig. 1. Anterior view, ♂

2. Occiput, ♀

3. Posterior view, ♂

4. Lateral view

5. Tentorium, lateral view

6. Tentorium, lateral view

Plate II -- MOUTH PARTS , ABORAL VIEW (7, 9, 11); ADORAL VIEW (8, 10, 12)

Figs.7 & 8. Clypeus

9 & 10. Mandible

11 & 12. Hypopharynx

Plate III -- MOUTH PARTS, ABORAL VIEW (13, 15); ADORAL VIEW (14; 16)

Figs. 13 & 14. Maxillae

15 & 16. Labium

Plate IV -- PROTHORAX & NECK

Fig. 17. Dorsal view

18. Ventral view

19. Lateral view

20. Posterior view

Plate V -- SYNTHORAX

Fig. 21. Lateral view

22. Internal view of dorsal portion

23. Dorsal view

Plate VI -- SYNTHORAX & LEGS

Fig. 24. Ventral view

25. Internal view of ventral portion

26. Posterior view of X-section behind metathoracic furcal pits

27. Anterior view of X-section behind metathoracic furcal pits

28. Prothoracic leg, ♂

29. Prothoracic tibia, dorsal view, ♂

30. Pretarsus, ventral view

Plate VII -- WINGS & ABDOMEN

Fig. 31. Fore wing

32. Hind wing, ♂

33. Basal segments, dorsal view, ♀

34. Basal segments, lateral view, ♀

35. Sternites VI & VII, ♂

36. Sternite II, ♀

37. Sternite III, ♀

38. Sternite V, ♀

39. Sternite VII, ♀

Plate VIII -- MALE ACCESSORY SEXUAL ORGANS

Fig. 40. Basal abdominal segments, ventral view

41. Ventral view, penis & right hamules removed

42. Lateral view

43. Anterior lamina & hamules

44. Penis, lateral view

Plate IX -- TERMINAL ABDOMINAL SEGMENTS

Fig. 45. Dorsal view, ♂

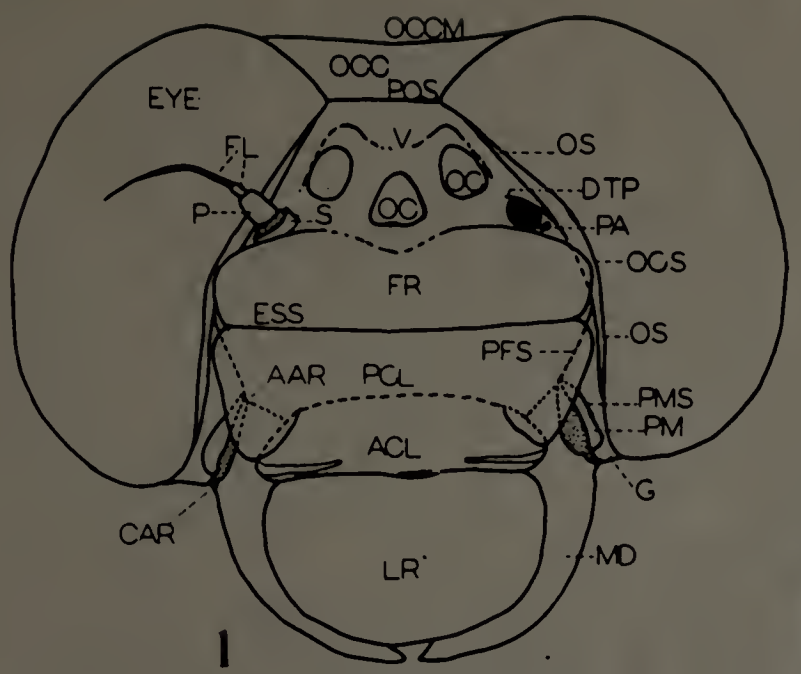
46. Ventral view, ♂

47. Ventral view, ♀

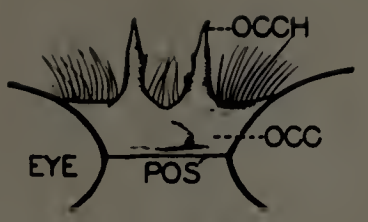
48. Dorsal view, ♂

49. Lateral view, ♀

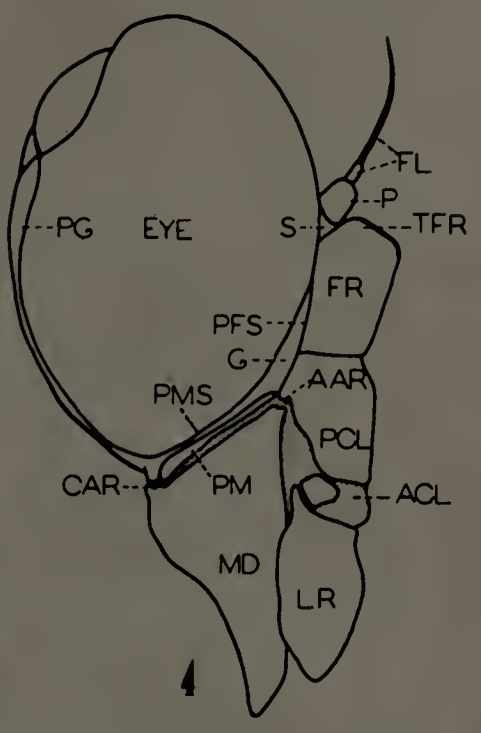
50. Lateral view, ♂



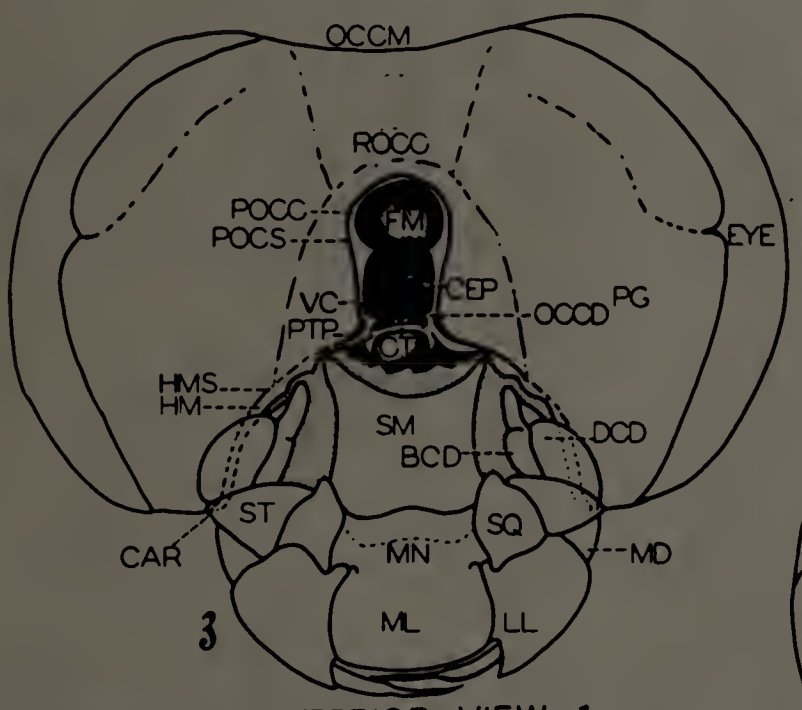
1 ANTERIOR VIEW, ♂



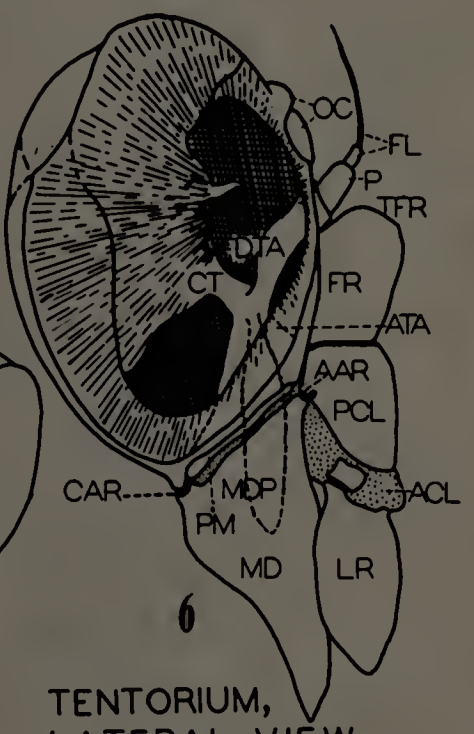
2 OCCIPUT, ♀



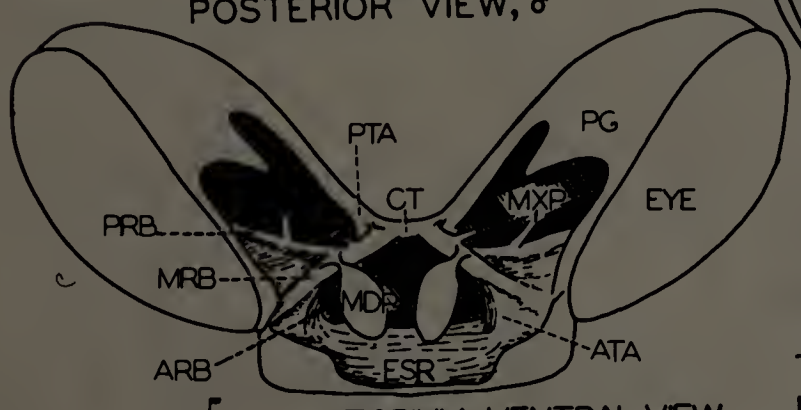
4 LATERAL VIEW



3 POSTERIOR VIEW, ♂

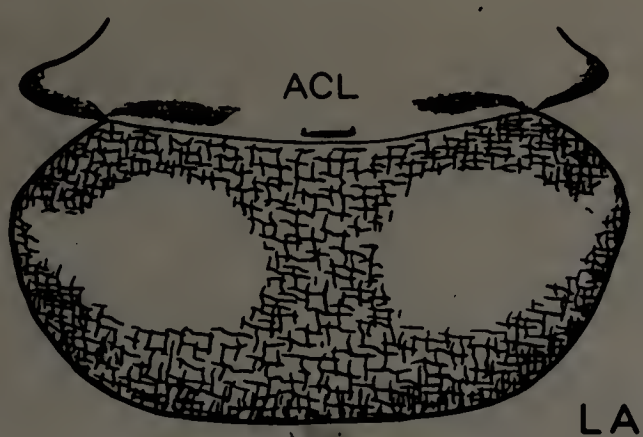


6 TENTORIUM, LATERAL VIEW



5 TENTORIUM, VENTRAL VIEW

PLATE 1 — HEAD



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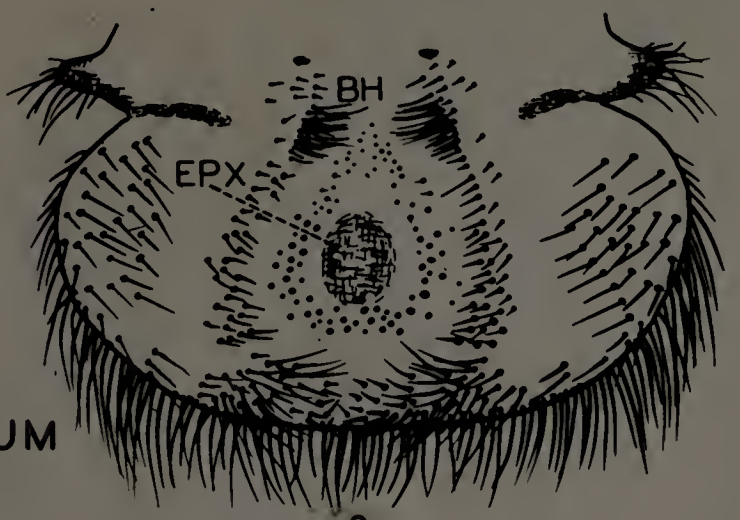
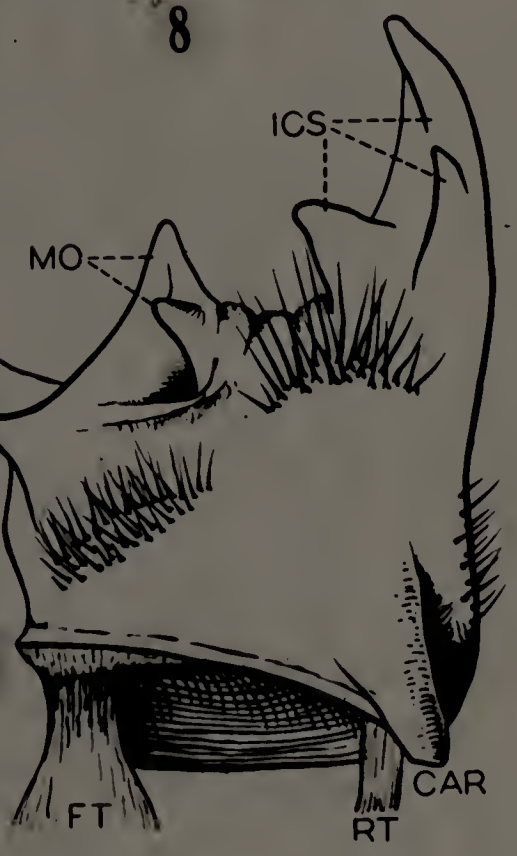


LABRUM

8

9

MANDIBLE



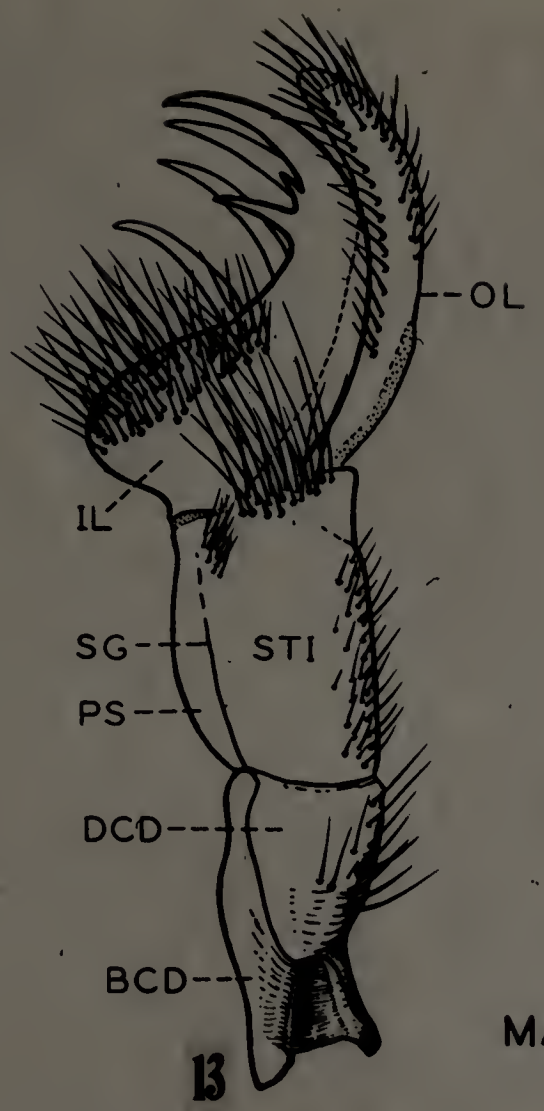
10

11

HYPOPHARYNX

12

PLATE II — MOUTH PARTS, ABORAL VIEW (7,9,11); ADORAL VIEW (8,10,12)



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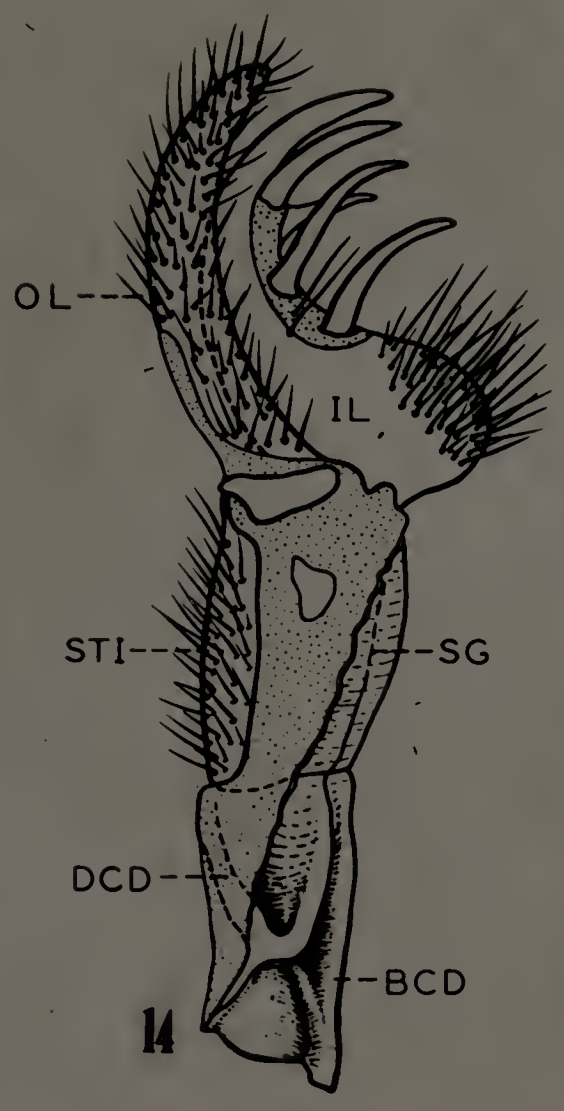
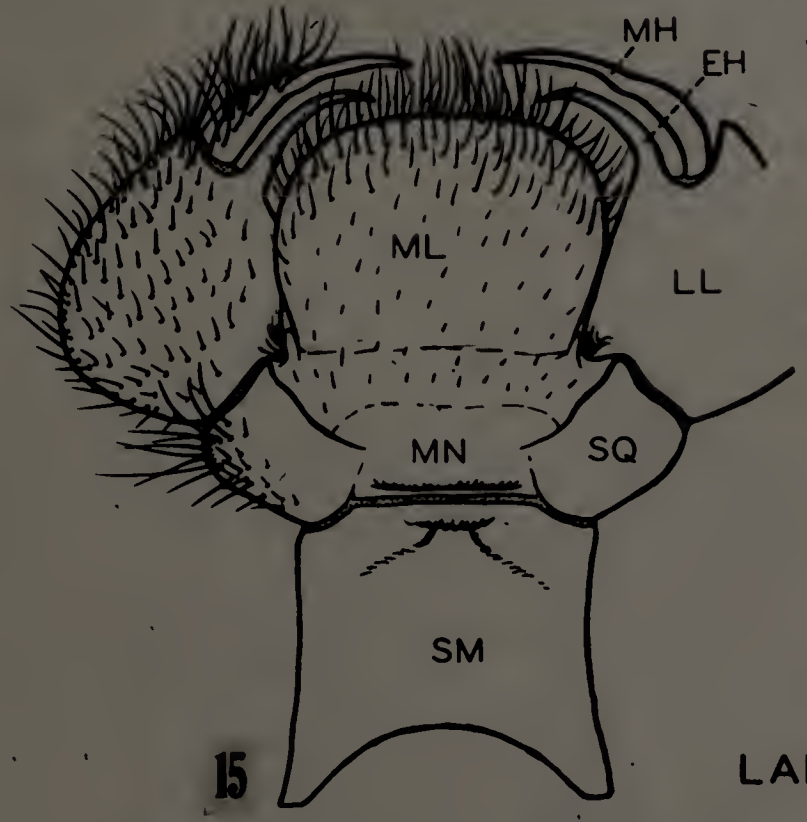


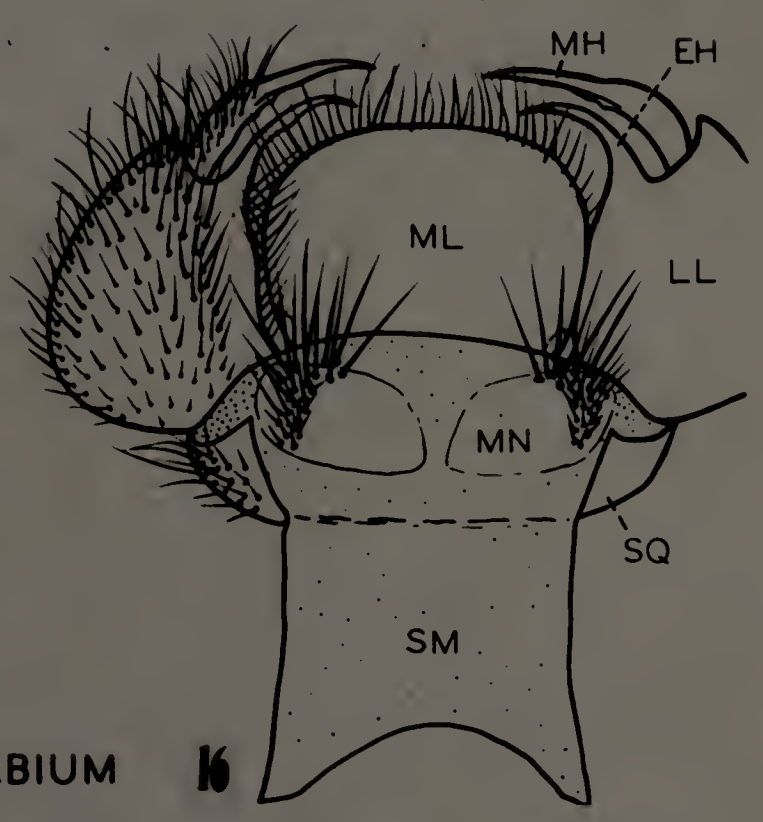
14

MAXILLA



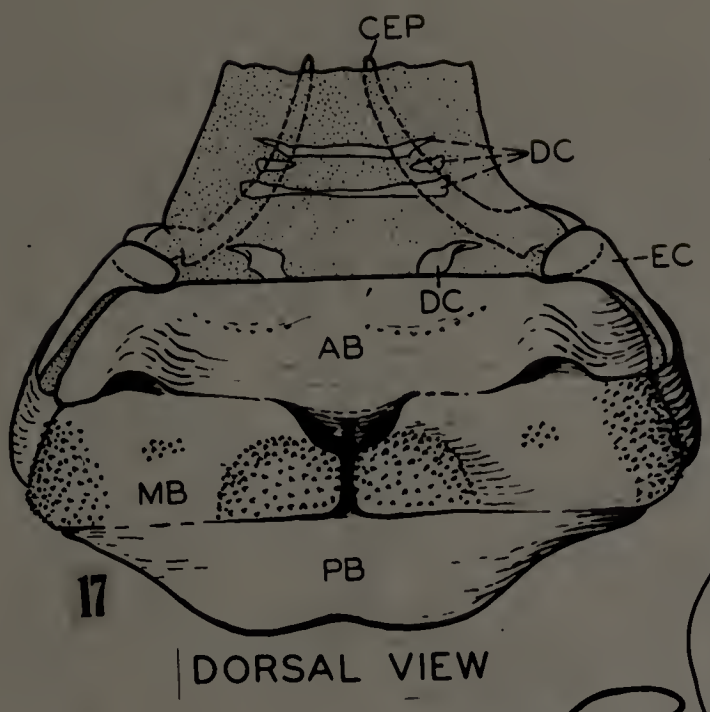
15

LABIUM



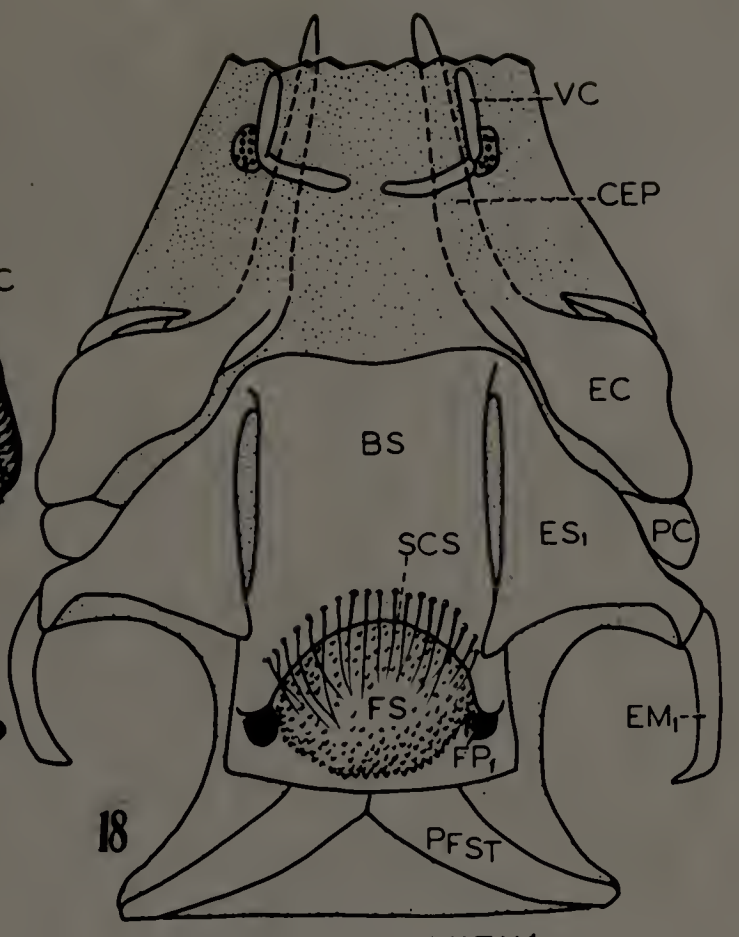
16

PLATE III – MOUTH PARTS, ABORAL VIEW (13,15); ADORAL VIEW (14,16)



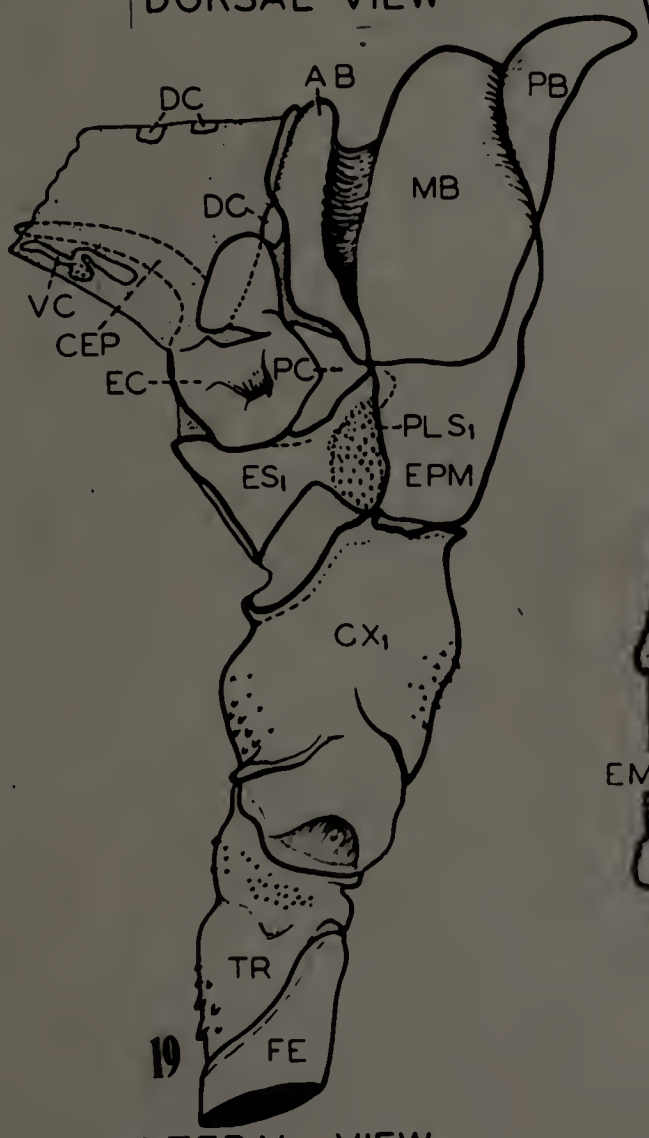
17

DORSAL VIEW



18

VENTRAL VIEW



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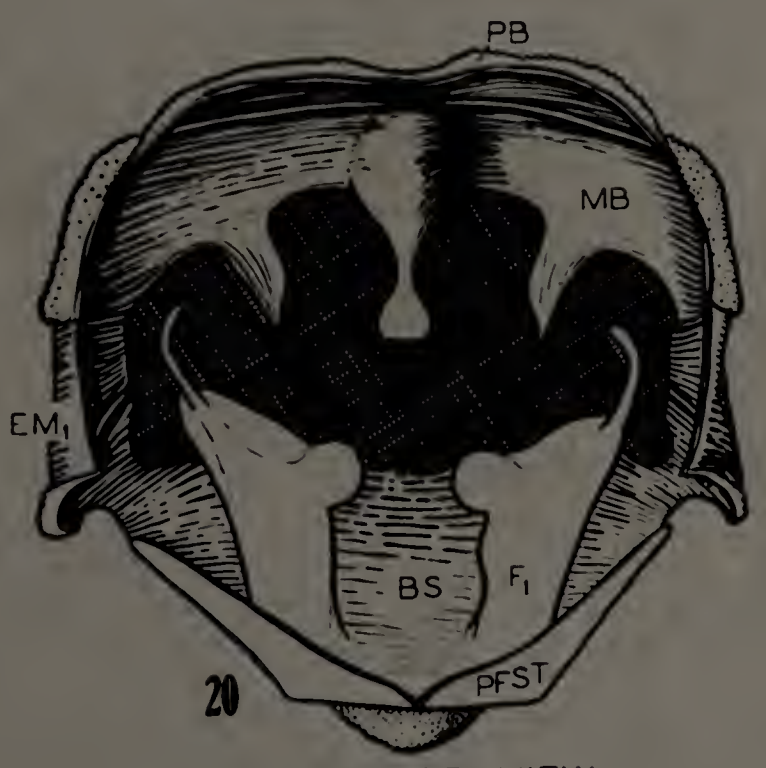
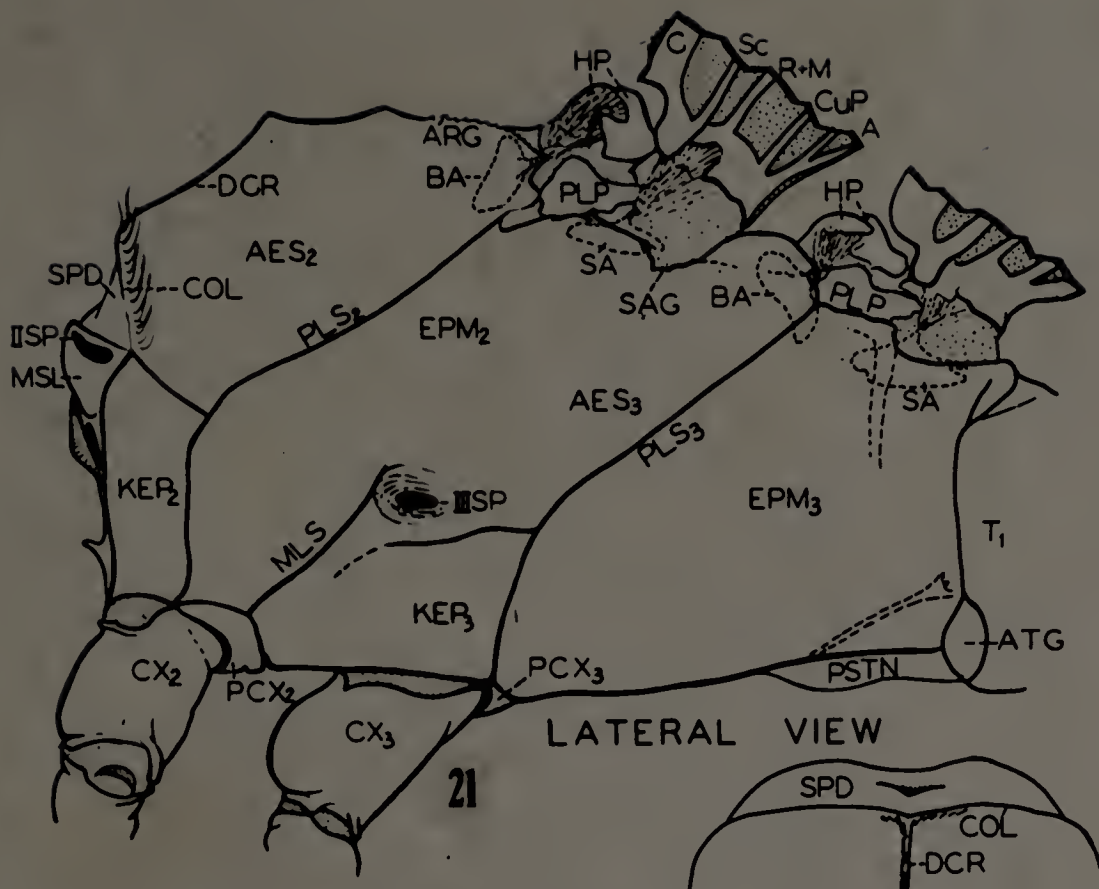
LATERAL VIEW

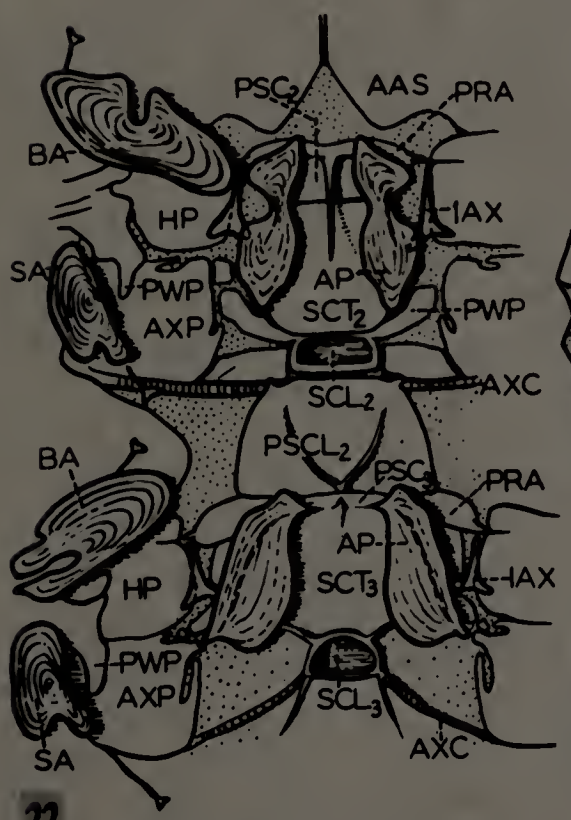


20

POSTERIOR VIEW

PLATE IV - PROTHORAX & NECK





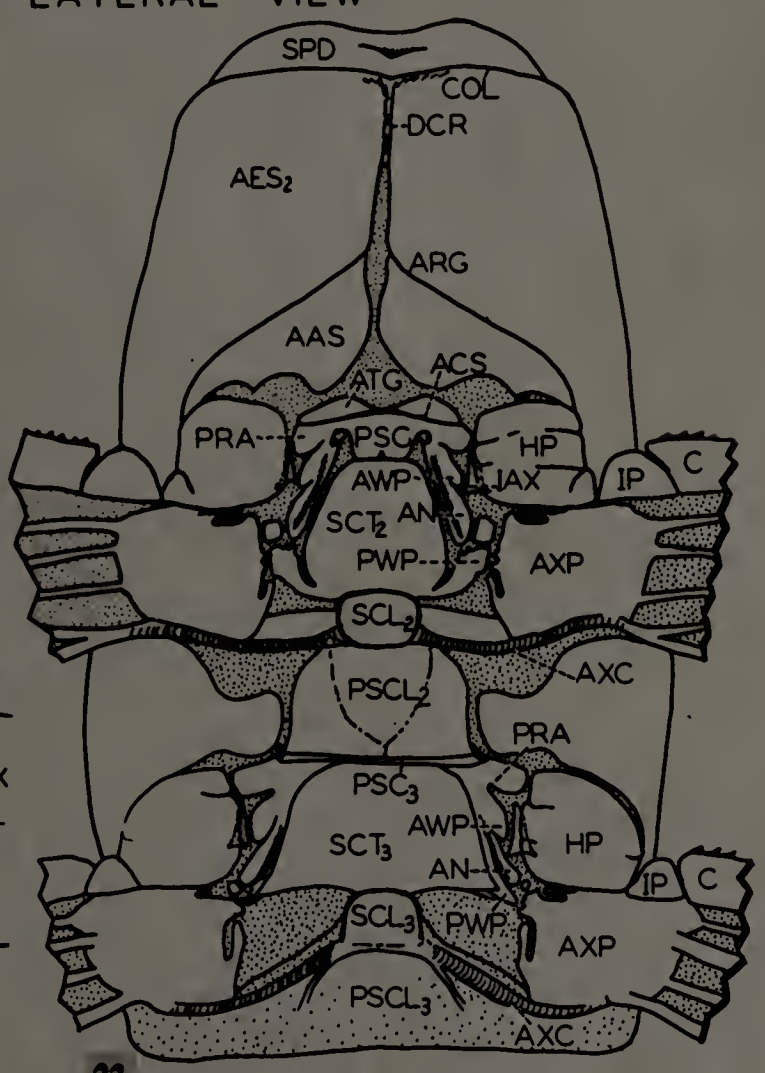
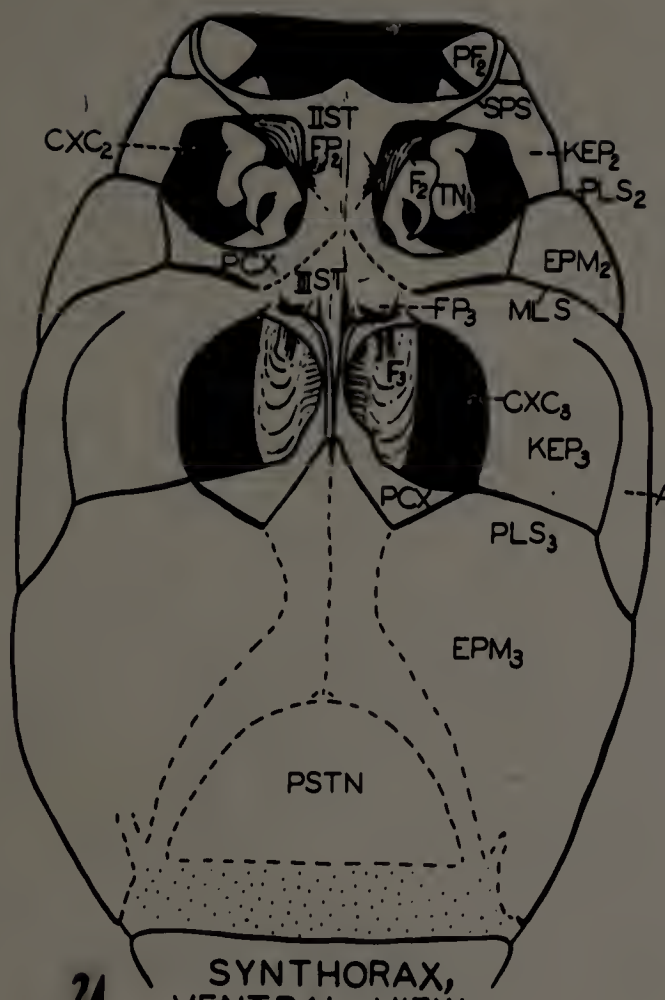
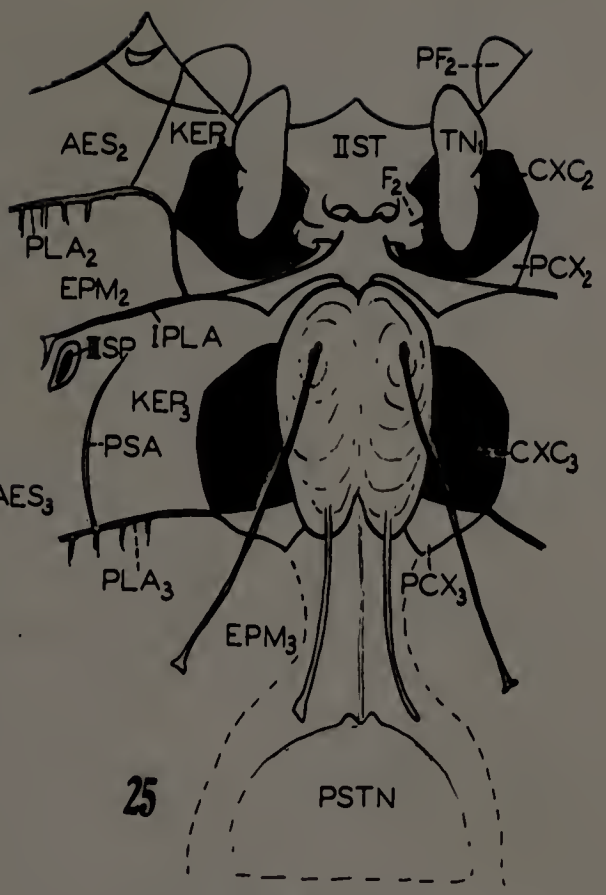


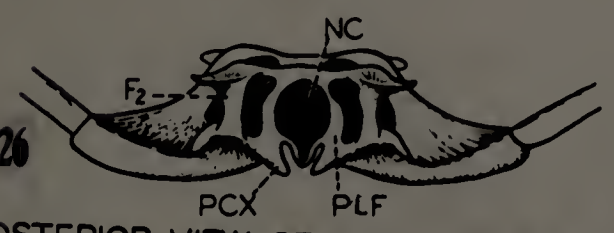
PLATE V – SYNTHORAX



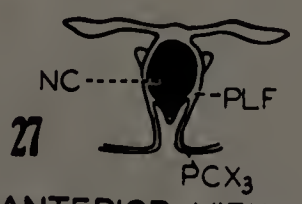
24 SYNTHORAX, VENTRAL VIEW



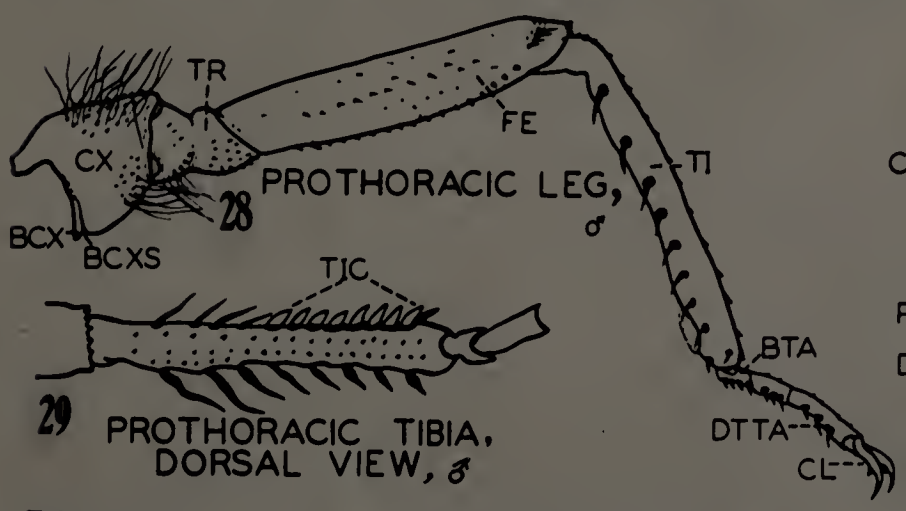
25 INTERNAL VIEW OF VENTRAL PORTION



26 POSTERIOR VIEW OF X-SEC. BEHIND FP_3

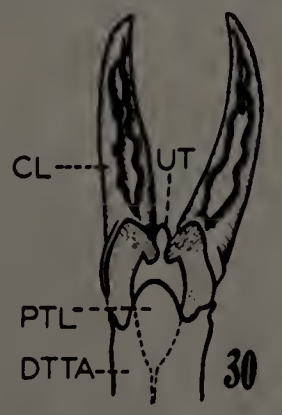


27 ANTERIOR VIEW OF X-SEC. BEHIND FP_3



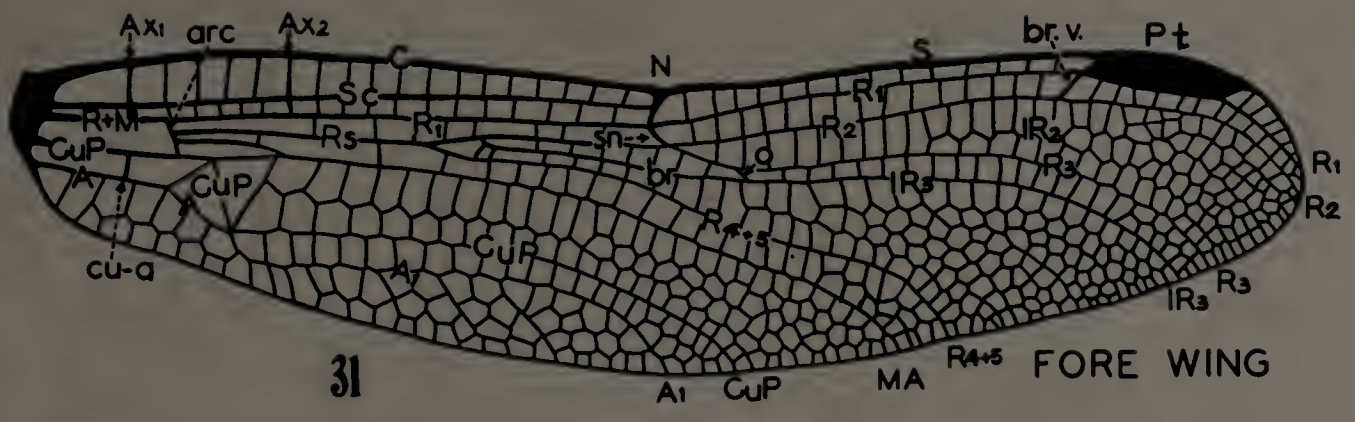
28 PROTHORACIC LEG, ♂

29 PROTHORACIC TIBIA, DORSAL VIEW, ♂

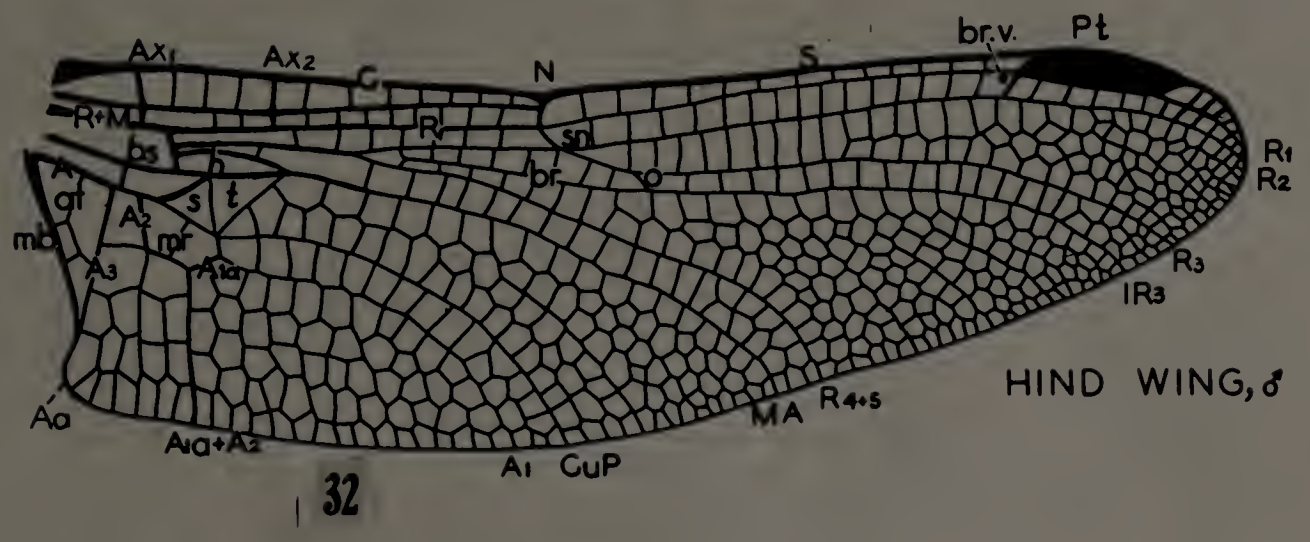


30 PRETARSUS, VENTRAL VIEW

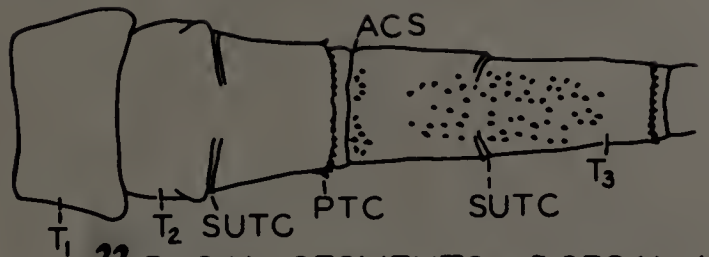
PLATE VI — SYNTHORAX & LEGS



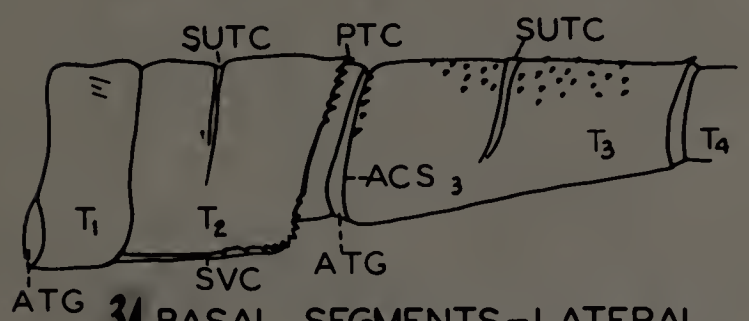
31 FORE WING



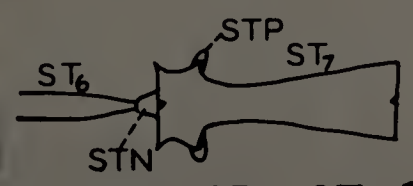
32 HIND WING, ♂



33 BASAL SEGMENTS - DORSAL VIEW, ♀



34 BASAL SEGMENTS - LATERAL VIEW, ♀



35 STERNITES VI VII, ♂

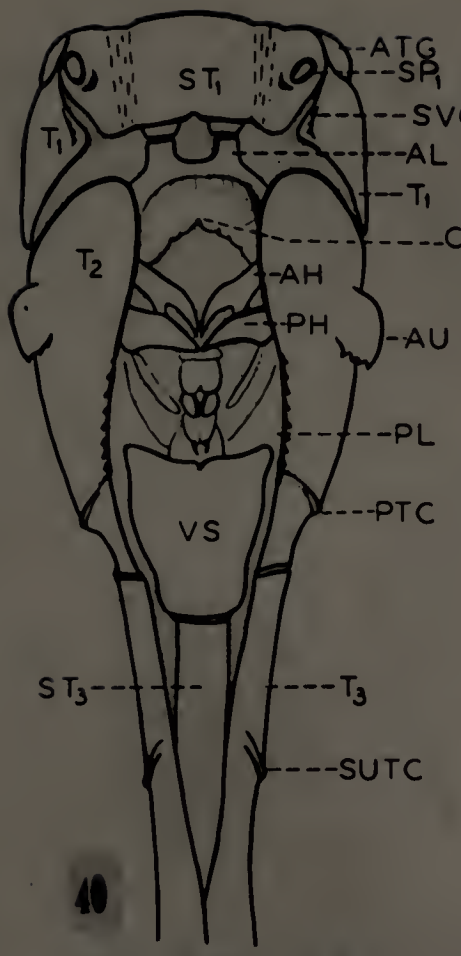
36 STERNITE II, ♀

37 STERNITE III, ♀

38 STERNITE V, ♀

39 STERNITE VII, ♀

PLATE VII — WINGS & ABDOMEN



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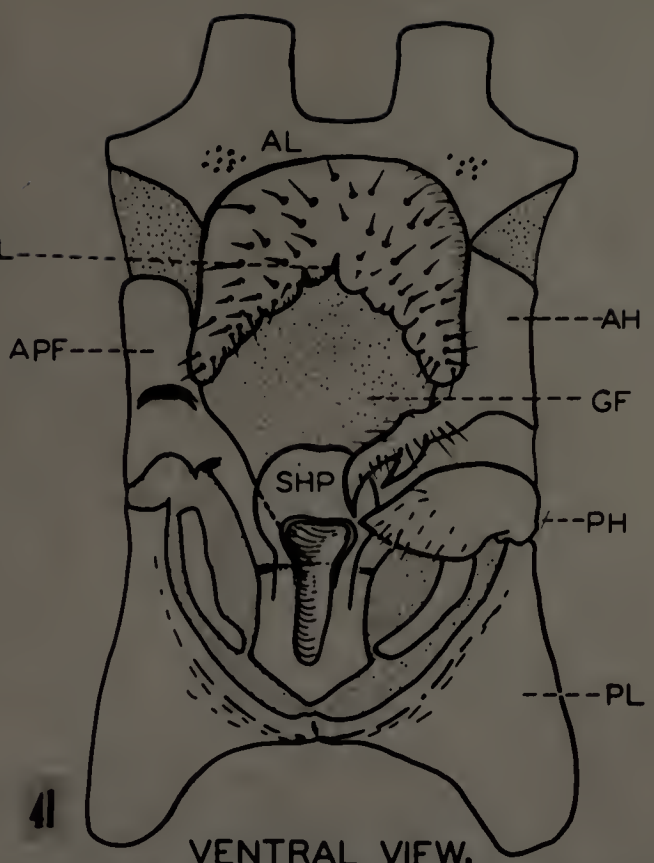
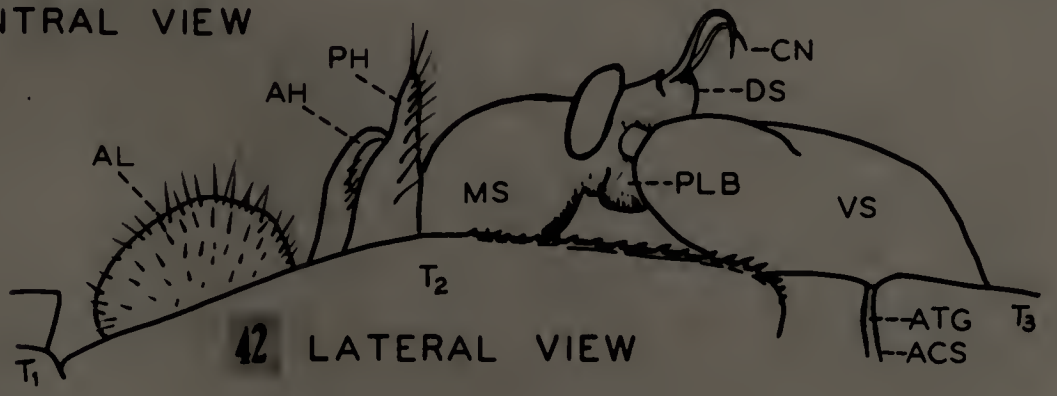
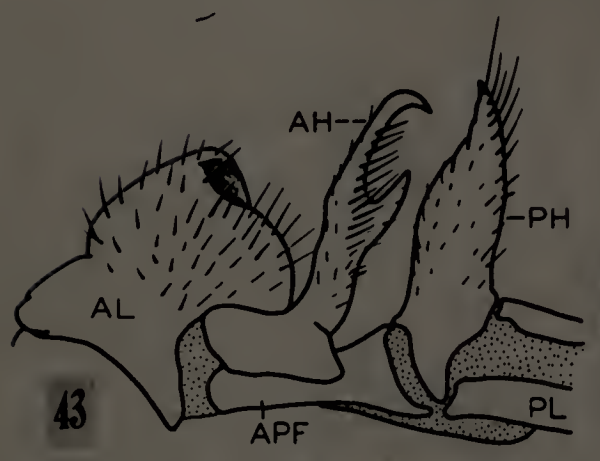


41 VENTRAL VIEW, PENIS & RIGHT HAMULES REMOVED

VENTRAL VIEW



42 LATERAL VIEW



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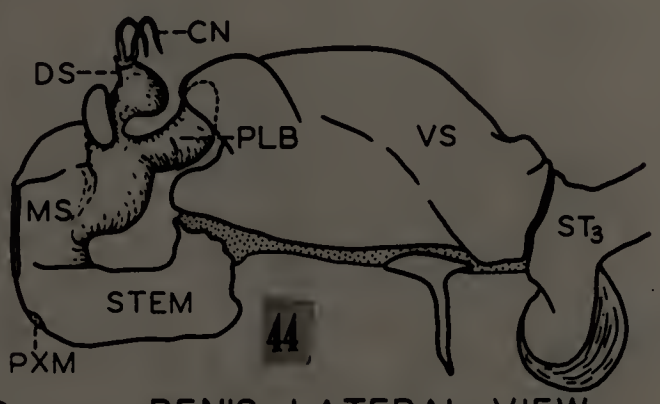

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ANTERIOR LAMINA & HAMULES

PENIS, LATERAL VIEW

PLATE VIII — ACCESSORY SEXUAL ORGANS, ♂

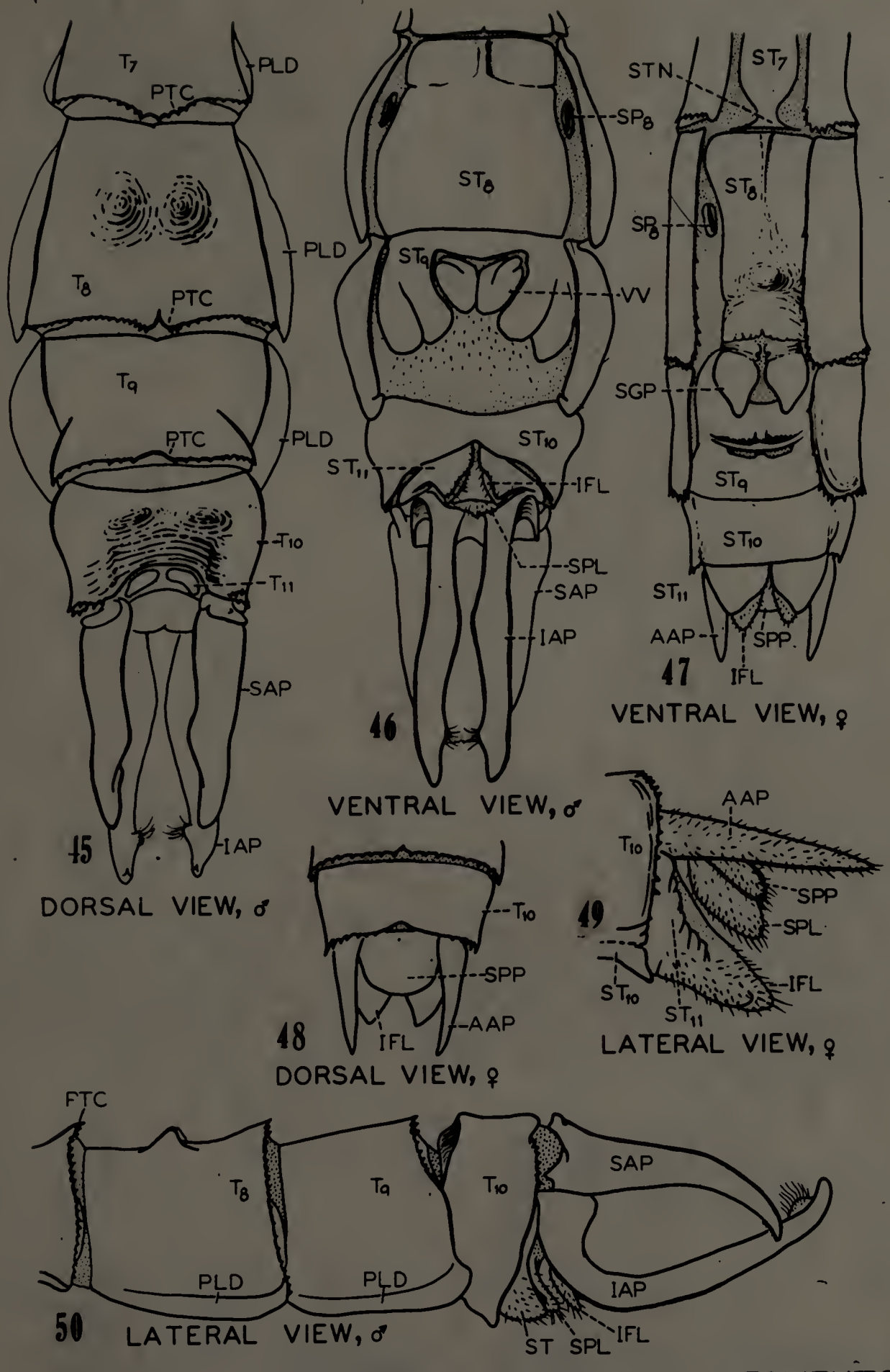

PLATE IX - TERMINAL ABDOMINAL SEGMENTS

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Graduate Committee

Date